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FUNDAMENTALS OF PLANT-BREEDING

FUNDAMENTALS OF PLANT-BREEDING

BY

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PREFACE

The most fundamental material problem that confronts the American people is the problem of food production, and it is of interest to know what is being done toward solving it. When it is realized that the population of this country is increasing much faster than its food production, it is obvious that such disparity must not continue. To state the problem is to raise the question whether it is possible to increase food production, and whether anything has been accomplished toward realizing such a possibility.

It has been said that agriculture is the oldest art and the youngest science. So old is the art that those who practice it are in danger of shutting their eyes to what they may regard as impractical science, and yet the recent achievements of science in the study of heredity have made possible a revolution in plant-breeding. Along with the development of scientific plant-breeding, there has developed also an increasing knowledge of the soil, which in most of the history of agriculture has been treated empirically. The result is that it is possible now to obtain results from plants which were never dreamed of in the older agriculture. It is the purpose of this book to give an account of these possibilities.

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PREFACE

The scientific work that has formed the basis of the recent practical achievements in plant-breeding needs to be interpreted to a very large audience, an audience intensely interested, but with no technical training. Important results are being obtained that affect the welfare of everyone, and to some understanding of these results the public should be admitted. The public has received much information as to the needs and possibilities of agriculture that is partial, and often misleading. In no subject is there more misinformation as to the things that are essential, and this has arisen largely from a failure to appreciate all the factors involved. The need of an interpretation of the recent advances in plant-breeding is emphasized further by the growing interest in agriculture, which has extended beyond the professionally interested agricultural colleges, and is penetrating secondary schools everywhere.

In addition to this growing audience of interested citizens, and of those interested in general education, there are the students of agriculture, and the large body of practical farmers who may find in this book some perspective for their work, and a better appreciation of the importance of the task they have undertaken. Furthermore, those interested chiefly in the scientific aspects of botany should become familiar with the important practical applications of their subject.

In short, this book is addressed to those who wish a simple statement of evolution and heredity; who wish information concerning the revolution in plant-breeding; or who wish a general introduction to the fundamental principles underlying agriculture. This should include citizens interested in the things that make for the public welfare, farmers, students of agriculture, teachers in the public schools, and botanists.

John M. Coulter.

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FUNDAMENTALS OF PLANT-BREEDING

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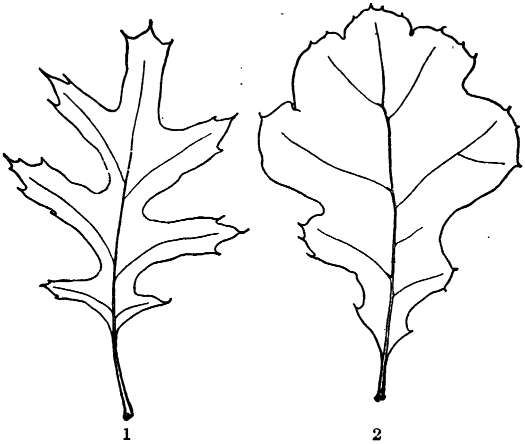
CHAPTER I

VARIATION IN PLANTS

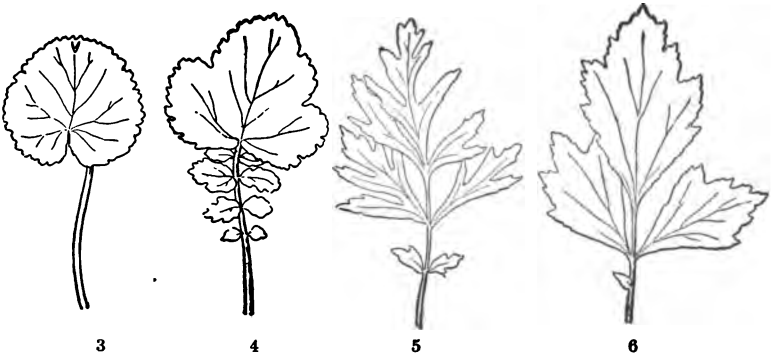
In order to understand how it is possible to improve plants or to produce new ones, one must appreciate first how plants vary. If all the individual plants of a wheat field, for example, were exactly alike, there would be no chance to improve them or to produce from them new kinds of wheat. In fact, no two plants of a wheat field are exactly alike, although they may appear so to the untrained eye. We recognize individual differences in plants and animals only as we become well acquainted with them. For example, we have become so well acquainted with the individual differences of men that no two of them look to us exactly alike. If we were as well acquainted with the differences of wheat plants, no two of them would look exactly alike. We cannot recognize individual differences equally well even in all races of men. The individuals in a group of Chinese look more alike to most of us than do the individuals in a group of our fellowcitizens. This suggests that one must be well acquainted with the distinguishing marks of a group of plants or of animals before he can appreciate how much they can vary. The first fact to appreciate, therefore, is that no two plants are exactly alike, even though they belong to the same species. They belong to the same species on account of their similarity, but at the same time each plant has an individuality of its own, which means that it differs in certain particulars from every other individual. The improvement of plants and the production of new ones, therefore, depend upon the fact of individuality, which means that variation is universal.



FIGS. 1-2.—Leaf variation in the black oak (*Quercus velutina*): Fig. 1, an upper leaf, exposed to strong sunlight; Fig. 2, shade leaf, from a lower branch of the same tree.—From Coulter, Barnes and Cowles' "Textbook of Botany."

VARIATION IN PLANTS

Variations in plants are of all degrees, from very small ones to very large ones. The variation may be so small that only the trained eye can recognize it, or it may be so large that anyone can recognize it. For example, two plants of the same species may differ so little in the breadth of their leaves that the difference would not attract attention; while two other plants of the same species may differ so much in the breadth of their leaves that they might raise the question whether they are really the same kind of plant. There is no more variable structure than leaves, a fact suggested in such illustrations as the leaves of the black oak (Figs. 1 and 2) and of the common *Geum* (Figs. 3-6). Variations are often grouped as small and large variations, and there have been differences of opinion as to which kind is used



FIGS. 3-6.—Leaf variation in *Geum virginianum*.—From Coulter, Barnes and Cowles' "Textbook of Botany."

in producing new forms. It is obvious that a grouping on the basis of degree of variation is indefinite, for it is often impossible to determine when to stop calling a variation small and to begin calling it large.

There is a much more fundamental difference in variations, however, than difference in degree. Suppose an individual plant varies from others of its kind in having broader leaves. The difference in breadth may be small or great, but the kind of variation will be determined when the seeds from the broader-leaved plant produce other plants. If these new plants of the next generation do not all continue the broader leaves, but produce also leaves of the usual breadth, the variation is called a *fluctuating variation.* This phrase implies that the variation fluctuates from generation to generation, now appearing and now disappearing. In other words, it is not constant. It may be likened to a pendulum that swings back and forth through a certain range, but never remains fixed at any one point. It advances in a certain direction, but it always comes back. If the new plants of the next generation, however, all produce the broader leaves, and this character continues generation after generation, it is called a *constant variation* or *mutation.* The range through which the pendulum swings has been changed permanently, and it does not come back to the narrower leaves. The significant difference among variations, therefore, is not that they are large or small, but that they are fluctuating or constant.

A large variation may be a fluctuating one, and a small variation may be a constant one A fluctuating variation cannot travel very far, for it has its limits and is always coming back; while a series of constant variations may travel any distance, for the limits of variation change.

The contrast between fluctuating and constant variation may be made clearer by an illustration. Imagine a wild potato plant producing a crop of small tubers somewhat variable in size. This means that there is a variation toward larger tubers. If one of the larger tubers is planted and a second crop of tubers is produced, the new crop will determine whether the variation toward largeness is a fluctuating or a constant one. If the new tubers are just like those of the first crop, that is, a mixture of smaller and larger ones, the variation is fluctuating. On the other hand, if the second crop contains only tubers of a larger size, the variation is constant. It is obvious that constant variations are especially useful in securing improvements that are permanent; while fluctuating variations are very uncertain in their results.

It must not be supposed that all kinds of plants are equally variable. Some are quite rigid in their characters, so that individuals of the same kind resemble one another as closely as individuals can. In other words, the range of the pendulum is very small. Not only do such plants maintain this narrow range of variation in nature, but they usually resist all attempts to make them vary more widely under cultivation. Other plants are exceedingly variable, so that individuals of the same kind may be remarkably different; in other words, the range of the pendulum is very large. Such plants are called *plastic,* because they can be molded into a great variety of forms. It is evident that, in improving plants or in producing new ones, the plastic plants are much more likely to respond to culture than the rigid ones. It must be remembered, however, that in producing new forms we wish plasticity, but after a desirable form is produced we wish rigidity.

The breadth of leaves has been used to illustrate variation, but it should be realized that all organs of plants vary and they vary in all directions. Leaves, stems, roots, flowers, and fruits all vary, but they do not necessarily all vary together. The picture of variation to carry in mind, therefore, is that of all parts of a plant varying more or less in any direction. When a plant is produced by a seed it will resemble its parents in a general way, but its different parts (organs) will vary more or less in character from the corresponding parts of the parents. This is what gives to the new plant an *individuality* of its own, by which it is distinguished from all other plants of the same kind. This variation occurs not only in the appearance of the conspicuous organs mentioned, but also in the internal structures; so that the plant varies in structure as well as in form. Certain organs and certain structures are more subject to variation than others because they are more related to external conditions. For example, leaves are very directly related to varying conditions of water supply, light, and temperature, and in most cases may be expected to respond in varying dimensions, forms, and structures in a more obvious way than does a seed-vessel. This illustration must not be understood to imply that all variations are responses to changing external conditions. There are other causes of variation that will be considered later. The fact to be enforced at this point is that, while all organs of a plant vary, some of them are more rigid than others.

It must not be supposed that variation in form and structure is the only kind of variation, although it is the kind that makes plants appear different. Two plants may appear to be almost identical in structure and yet differ much in quality. This may be appreciated when the differences in the qualities of fruits and of grains are remembered. Wheat and corn and apples, for example, vary, not only in the appearance of the plants, but also in the quality of the grain or fruit, and it is this variation that is the more important in the breeding of such plants. The different qualities of grains and fruits mean variation in plant products, that is, variation in the life processes. Variation in form and structure may be called *morphological* variation; while variation in quality is *physiological* variation. When one remembers the hundreds of kinds of apples of different flavors, and knows that they are all variations of a single kind of plant, he begins to realize how great physiological variation may be. If to this illustration is added the number of colors that a single kind of flower may produce, a variation that means different chemical products, the amount of physiological variation possible becomes as impressive as the possibility of morphological variation. It should be recognized, however, that physiological differences are not always associated with morphological differences. Since plant-breeding deals as much with quality as with structure, physiological variations which are invisible must be considered as carefully as the visible morphological variations. Since they may not be recognized by any external marks, physiological variations must often be discovered in other ways. An illustration of this situation may be obtained from the bacteria. Many bacteria which differ widely in their behavior seem to be exactly alike in appearance. It is well known, for example, that when certain bacterial diseases are suspected, physicians do not depend upon the microscope for the recognition of the bacteria, but upon "cultures," which show the physiological reactions characteristic of each species. In fact, bacteria are plants which are very little differentiated morphologically, but are very much differentiated physiologically. This serves to emphasize the fact that the breeding of our cultivated plants, which vary both morphologically and physiologically, involves a regard for both kinds of variation.

The most convincing evidence of variation in plants is obtained from cultivated plants. Many of these have been under cultivation throughout the recorded history of the human race, and some of them have been changed so much that their wild originals cannot be recognized with certainty. When removed from the wild state and brought under cultivation, plants are subjected to new conditions, and they have responded in the development of variations unknown in their wild state. For this reason they become so unlike their wild relatives that they seem like entirely different plants. It is not merely the new conditions that are responsible for the variations in cultivated plants which make them seem very different from their wild originals. Many of these variations doubtless occur in the wild state, but they are not perpetuated because they are not fitted for the wild conditions of living. Under the fostering care of man many variations are perpetuated which would have perished in nature. The artificial conditions of cultivated plants, therefore, not only probably induce certain variations, which otherwise would not occur, but chiefly they preserve and intensify variations which would perish in natural conditions. A good illustration of the power of a plant to vary extremely in several directions may be obtained from the species to which cabbage belongs (Figs. 7-14). All of our so-called "vegetables" have been very much modified under cultivation, the part that we prize, as tuber (potato), fruit (tomato), leaf (lettuce), etc., being most changed. The effect of cultivation upon the tendency of plants to vary will be presented more fully in the next chapter. Perhaps more impressive than the variations of cultivated plants, to most people, however, are the variations that have been secured in domesticated animals. When it is realized, for example, that the numerous races of dogs, varying so much in size and appearance as to suggest different species, have all descended from a common ancestral stock, the possibilities of variation seem to be without limit. The endless "breeds" of pigeons also are as different in appearance as related birds can be; while horses and cattle still further emphasize the possibilities of variation.

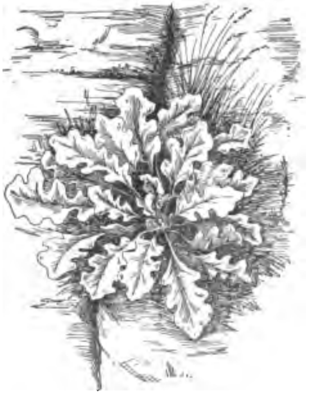
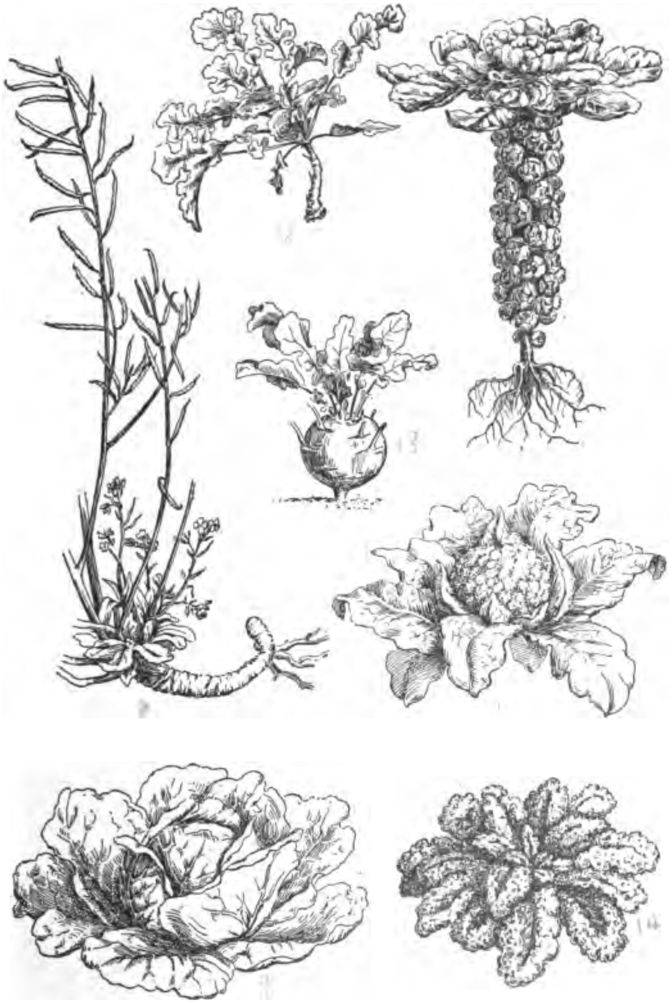


FIG. 7.—Wild cabbage growing on a cliff.—After BAILEY.

The fact of variation was recognized long before any attempt was made to discover the causes. The study of the classification of plants, which is the oldest phase of botany, encountered variations continually. In fact, the tendency of plants to vary was a constant contradiction of the old conception that species are cast in

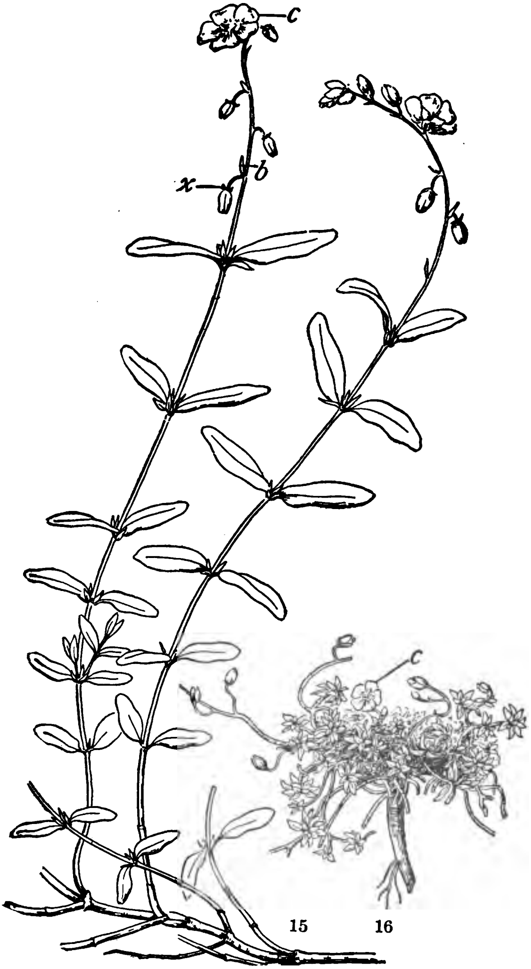


Figs. 8-14.—Some of the forms derived from wild cabbage: Fig. 8, wild cabbage; Fig. 9, cultivated cabbage; Fig. 10, cauliflower; Fig. 11, Brussels sprouts; Fig. 12, kale; Fig. 13, kohl-rabi; Fig. 14, collards.

rigid moulds. The old collectors who secured plants for herbaria searched for what were called ''typical'' representatives of a species, disregarding the numerous variations that did not seem to conform to what they thought the species ought to be. Accordingly herbaria are likely to give a wrong impression as to the variability of species. The selected individuals look quite uniform and quite distinct from the group of individuals representing another species. Species of plants thus came to represent pigeon-holes into which individuals were sorted; only such individuals as belonged in the pigeon-holes were kept; any individual that seemed to belong to more than one pigeon-hole was disregarded. Of course, when the conception of the fixity of species came to be questioned, and the idea of evolution began to develop, the varying individuals that could not be assigned to pigeon-holes became the most interesting. When Darwin developed his theory of natural selection as an explanation of evolution, he recognized the great variability of plants and animals, and based his theory upon this fact; and of course every theory of evolution depends upon it. However, neither Darwin nor any of the earlier exponents of evolution attempted to explain variation; they simply accepted it as a fact. It has been in connection with the study of heredity rather than of evolution that attempts have been made to explain variation.

One of the obvious causes of variation is a change in the conditions of living, a fact suggested by the remarkable variations that occur when plants are taken from the wild state and brought under cultivation. This is often called a "change of environment." Environment is a very complex thing, so that, when plants are said to change as environment changes, the particular factors in the environment that cause the change remain to be discovered. Experiments have shown that a change from one natural environment to another causes plants to vary, as well as a change from a natural environment to the artificial one of cultivation. For example, seeds from plants of the lowlands when sown in alpine conditions produce plants that are not only much lower in stature, but also very different in general habit (Figs. 15 and 16); and if the transfer is made from alpine to lowland conditions, the reverse result is obtained. It has been found that certain plants transferred from the interior to the seacoast become succulent (fleshy); while succulent plants of the seacoast transferred to the interior lose their succulence.

But plants vary even when the conditions of living are not changed; and, therefore, in addition to these external causes of variation, which may be said to result in fluctuating variations, there are also internal causes connected with inheritance. Since no two individuals are exactly alike, and since usually two individuals are concerned in the production of a seed, the plant that comes from the seed will contain a combination of char-



FIGS. 15 AND 16.—Leaf and stem variation in *Helianthemum vulgare;* Fig. 15, a plant of the lowlands; Fig. 16, a plant grown in an alpine garden from a part of the same plant shown in Fig. 15. —From Coulter, Barnes and Cowles' "Textbook of Botany."

acters from the two parents. Each individual has a new combination of characters, and for this reason no two individuals are exactly alike. The more unlike the two parents are, the more obvious become the variations in progeny, so that what seem to be really new kinds of plants may be produced. For example, two individuals of the same species usually produce progeny that do not differ very much from the parents; but two individuals of different species produce progeny that may differ very much from either parent. When the parents do not belong to the same species or variety, their union is called *crossing,* and the result is a *hybrid.* The artificial production of hybrids is one of the common methods of obtaining new forms, but there is doubtless much crossing in nature, resulting in many hybrids and many new forms. In fact, it is very difficult to determine whether a given wild plant is a pure strain or a mixture of two or more strains. In nature, therefore, variation arises not only from the natural pairing of similar individuals, but also from the crossing of unlike individuals.

However, environment and inheritance taken together do not explain all the facts of variation. Most plants possess other methods of propagation than by seeds. For example, the potato is propagated by tubers, so that new individuals arise from a single parent stock. This is called *vegetative multiplication,* as distinct from *sexual reproduction.* In such cases it is found that the progeny vary less than if they came from seeds; in other words, they are more constant. But still they vary to some extent, although the environment has not changed, and there has been no combination of characters from two parents. All of this goes to show that, while we know some of the general causes of variation, there still remain causes that have eluded us.

An important fact to remember in connection with variations is that, aside from those that appear in response to a changed environment, there are also those that appear without any reference to the environment. In fact, probably most of the variations that arise through inheritance do not find external conditions in nature favorable for their continuance. In other words, they are born into an "unfriendly world." This means that a majority of the variations which appear do not survive. Obviously the reason why cultivated plants become very different from the wild originals is not so much that the conditions of cultivation induce these particular variations as that they preserve them. It is for this reason, also, that when cultivated plants are uncared for, which means left to nature, they either disappear or "run back," for the natural conditions do not permit such variations.

The adjustment of plants to their environment is usually spoken of as their *adaptation*. Certain plants are said to be adapted to desert conditions, others to swamp conditions, others to alpine conditions, etc. If this merely implies that only certain kinds of plants can live in these various conditions, then of course plants are adapted to various kinds of environment. But if adaptation is taken to mean that the plants have gradually worked out structures suited to these various conditions of living, then it cannot be true, for plants must be "adapted" from the start to live at all. Their "adaptations" may become more efficient as they continue to live in the conditions that require them, but they cannot start these adaptations after they begin to live in the conditions. A plant already "adapted" can be found only among the innumerable variations that are continually appearing, and such plants survive in these conditions, while the others do not. Adaptation, therefore, is the *selection* of suitable forms rather than their *production*.

SUMMARY

Variation is a universal fact, no two individuals being exactly alike. It occurs in every degree, in all directions, in all structures, and is physiological as well as morphological; it is either fluctuating (coming and going) or constant (inheritable); it is much freer in some plants and structures (plasticity) than in others (rigidity); its best evidence is to be found in the great changes in every direction induced or preserved in plants when transferred from the conditions of nature to the conditions of cultivation; its causes are known to include changes in the conditions of living (environment) and new combinations of characters through inheritance, but it occurs also when neither of these causes is operating; it results in permanent forms only in the case of forms that are suited to the conditions of living, and these forms may be said to be adapted.

CHAPTER II

THE THEORY OF NATURAL SELECTION

It seems to be a far cry from a theory of evolution to such practical things as the improvement of plants and the production of new ones, but it was the work upon evolutionary theories that laid the foundation for the scientific plant-breeding of to-day. Conspicuous among the theories that have had this result are Darwin's theory of *natural selection* and DeVries' theory of *mutation,* and both of these theories should be understood in order to appreciate their bearing upon the revolution in plant-breeding.

It should be understood that the idea of organic evolution is as old as our records of men's thoughts, and that no one can be cited as its author. The names that have come to be associated with it are the names of men who have attempted to explain it. It is one thing to accept a fact, and a very different thing to accept some proposed explanation of it. Organic evolution is accepted by biologists as a fact, but no explanation as yet has seemed convincing to all of them. This has led to some misunderstanding among those who are not biologists. For example, they may have heard that certain biologists are criticizing Darwin's explanation of evolution by natural selection, and since in their minds Darwin is responsible for the idea of evolution, they infer that biologists are giving up evolution. It is obvious that Darwin's explanation and all other explanations that have been proposed could be criticized or even disproved, and still the fact of organic evolution remain to be explained.

Speaking in a very general way, the history of organic evolution as a subject may be divided into three periods. The first period was that of *speculation,* and it came to an end approximately with the eighteenth century. During that period, organic evolution was a philosophical speculation rather than a scientific subject; it rested upon abstractions rather than upon any definite body of facts. With the beginning of the nineteenth century evolution became a scientific subject, this second period being that of *observation.* In this period Darwin dominated, and all explanations of evolution rested upon an extensive body of observations. With the opening of the twentieth century the history of evolution passed into its third period, that of *experimentation,* and the subject is living in that period to-day. Putting the study of evolution upon an experimental basis must be regarded as a contribution by DeVries of more importance than his theory of mutation.

It is evident that in this discussion the speculative stage of evolution need not be considered, but we are very much concerned with the two scientific stages, each of which will be presented by its most conspicuous theory.

The theory of natural selection was announced by Darwin in 1858, and was published in full, with the evidence upon which it was based, in 1859, in the volume entitled "The Origin of Species." Probably no scientific book ever produced a more profound impression. It came at a psychological moment and was so convincing that it started a revolution not only in the method of attacking biological problems, but also in the method of attacking all problems. The great influence of this book upon all regions of intellectual endeavor was testified to in the various memorial volumes that appeared in connection with the Darwin centenary celebrations of 1909. It is easy to understand the theory as it developed through many years in Darwin's mind, and it is important to distinguish between the facts and what seemed to be the inevitable conclusion.

The first fact is the *ratio of increase.* Plants and animals increase by a geometrical ratio. For example, if a certain kind of plant produces an average of ten seeds, and each seed produces another plant, in nine or ten years there will be approximately a billion of these plants descended from the one individual. In this case 10 is the constant multiplier in the geometrical ratio. Of course, all seeds do not produce plants, and accidents happen to many of the plants produced, but if such plants were not interfered with their progeny would cover the earth's surface in a few years. Darwin used the elephant to illustrate the possible result of a geometrical ratio of increase even with a very low rate of reproduction. Assuming that the production of young begins at thirty years, that six young are produced in the course of the next sixty years, and that an elephant lives one hundred years, the result in seven hundred and fifty years is 19,000,000 elephants from a single pair. In the case of the lower plants and animals, in which the generations succeed one another with great rapidity, the theoretical result is astonishing. The impression left upon one is that the power of reproduction is a thing not to be encouraged, but repressed; that if it ever had a chance to express itself to the theoretical limit, the results would be prodigious. The power of reproduction, with its geometrical ratio of increase, may be likened to the ''genie of the bottle''; if the stopper is removed, the genie fills the heavens. Sometimes the stopper is removed to a certain extent, as when rabbits were transported to Australia and found a region free from their natural enemies. With the natural checks removed, the ratio of increase could express itself more fully, and rabbits swarmed over Australia. The weeds that have become a menace in this country now and then, as the march of the so-called Russian thistle across the Continent, are explained in the same way. They are immigrants that find their usual checks to increase removed, and the actual rate of increase more nearly approaches the theoretical ratio than it could in the native country of the plants.

The second fact is *competition,* or, as Darwin called it, "the struggle for existence." With a geometrical ratio of increase, even all of the natural checks to increase cannot prevent the appearance of many more individuals than can be supported. The result is severe competition among individuals at various stages in their development. In the higher plants the first great weeding out of individuals arises from the fact that very many seeds do not get a chance to germinate. The next weeding out results from the competition among seedlings, and from the unfavorable conditions surrounding seedlings. Relatively few seedlings that appear develop to maturity. For example, in a region of maples, the ground may be covered with maple seedlings in the spring, but hardly any of them ever become trees. The ratio of increase, therefore, results in competition.

The third fact is the *equilibrium of species.* If a certain kind of plant growing upon some natural area be observed season after season, it will be discovered that about the same number of individuals appear each year. When the ratio of increase is remembered, it is evident that competition has resulted in such a destruction of individuals that the number is not increased. In other words, the new individuals only replace the loss of old ones. This approximate uniformity in the number of individuals season after season is called the equilibrium of species. Every species in nature has established an equilibrium in a given set of conditions. When the conditions change the equilibrium is readjusted. If only enough individuals survive to replace the loss of old ones it is obvious that very many more individuals are produced than survive, for instead of a geometrical ratio of increase there is actually no increase. Thousands of seeds and eggs, seedlings and young animals, are produced for every one that survives. In other words, death is the rule, and life is the rare exception.

The fourth fact is *variation,* which was discussed in the preceding chapter. It was pointed out there that variation occurs in every individual, is often extensive, affects every region of the body, and occurs in every direction. In fact, it is variation that makes evolution possible, and every explanation of evolution has recognized this fact.

The fifth fact is the effect of *artificial selection.* Ever since men began to select certain wild plants for cultivation it has been known that these plants become changed under cultivation. In fact, in very many cases the changes have been so great that the wild originals are not recognized with certainty. If a plant were found in nature as different from other plants as are some cultivated plants from their wild originals, it would doubtless be regarded as a distinct species. The important fact is that cultivated plants have gradually changed in accordance with the needs or tastes of man (Figs. 7-14). This indicates that the changes have been guided by man, and it is important to know what he has done. The common potato may be used as an illustration. The wild potato grows in the mountain regions of the southwestern United States and Mexico, but it has very small tubers. Under cultivation the tubers have increased in size, and the method used has been to select the largest tubers for propagation. This selection for size, continued generation after generation, resulted eventually in such tubers as are cultivated now. It is evident that man took advantage of variation in the size of tubers, and guided it toward increasing size by a continuous selection for size. This selection is called artificial simply because it is done by man and not by nature. To show that man has really guided the changes in cultivated plants, and that they have not occurred in spite of his operations, the chrysanthemum may be used as a second illustration. In this case a structure very different from a tuber, namely, the flower, is selected for changing. The wild chrysanthemum has small flowers, but continuous selection for size has resulted in remarkably large flowers. Conversely, selection for smallness has resulted in producing a calla lily with much smaller flowers than those of the wild original (Fig. 17). Without multiplying illustrations further, it is evident that the variations of plants in cultivation have been guided by man in any direction

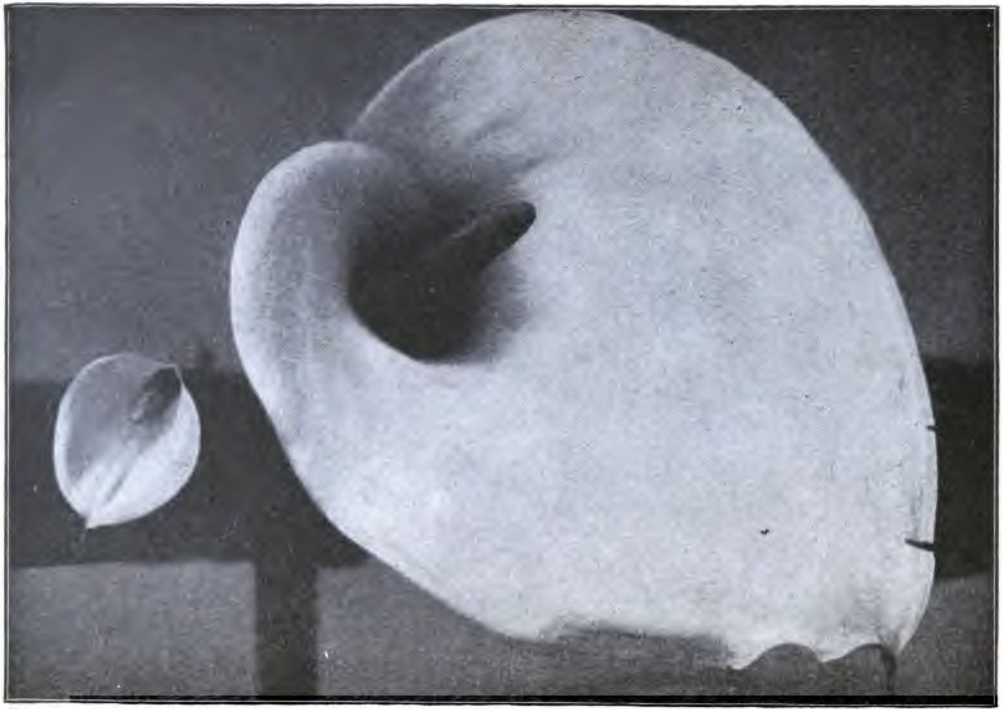


FIG. 17.—A small calla lily compared with one of normal size, produced by selection for smallness. —After DEVRIES.

of his choice, resulting in changes so great that the plants become remarkably different from their wild ancestors. The cultivation of plants has been called ''an experiment upon a gigantic scale,'' both as to time involved and the amount of material handled, showing how artificial selection may result in great changes.

With such facts before him, Darwin concluded that, if artificial selection can produce such changes, the same sort of selection is going on in nature, resulting in producing new species from old ones, no more change being demanded than artificial selection had often secured. Since such a selection is done by nature rather than by man, the appropriate name for it is *natural selection,* and this was Darwin's explanation of the origin of species, which is evolution. Nature can be personified as doing with native plants what the gardener does with cultivated plants, but it must be explained how nature can be said to ''select.'' The explanation is found in the series of facts given above. The ratio of increase results in the production of many more individuals than can survive. This leads to competition, the so-called ''struggle for existence,'' and by means of this competition nature selects. Since no two of the competing individuals are alike, the peculiarities of any survivor represent a favored variation, just as largeness has been a favored variation in the potato tuber or in the chrysanthemum flower. If the same variation is favored in succeeding generations, then nature is selecting for one kind of variation just as the gardener has done, and in time this variation will become large enough to represent another species. It is evident that nature must be as persistent in her choice as man has been, and Darwin concluded that this is secured by the fact that the individuals which win in the competition do so because they are better adapted (more "fit") to live in the existing conditions. So long as the conditions of living remain the same, therefore, the same variations will be selected for survival and thus continuous selection is secured. This is what Herbert Spencer called the "survival of the fittest," but which has also been called the "destruction of the unfit." The closing paragraph of "The Origin of Species" admirably summarizes the theory of natural selection:

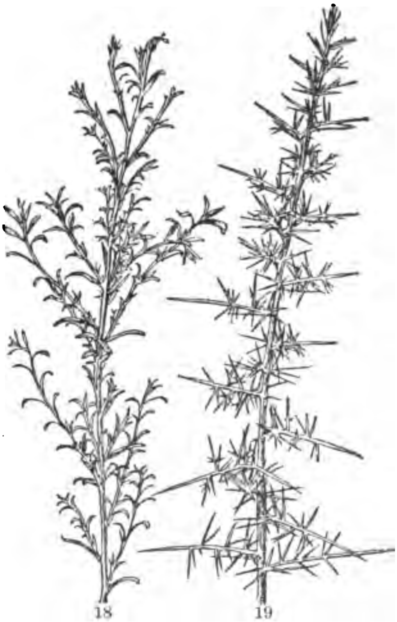
"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth and Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse: a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is a grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been and are being evolved."

In recent years more extensive work has uncovered some objections to Darwin's explanation of the process of evolution. These objections are not all pertinent to our purpose, for the fact remains that man can take advantage of variations and manipulate them for his own ends. Whether nature in some such way produces new species need not concern us. But it is important to know how far these objections may indicate the limitations of artificial selection as a method for improving old forms and securing new ones. If natural selection is unable to produce new forms, the inference is that artificial selection is limited in the same way. If the selection by nature is haphazard, without any reference to the "fitness" of the selected individual, then the so-called "adaptation" of plants to various conditions by artificial selection becomes a doubtful performance. If the changes attributed to natural selection are brought about in some other way, the inference is that artificial selection needs analysis to discover whether it is the real cause of the changes in cultivated plants.

An early objection to Darwin's explanation was that the forms produced under the guidance of man, when left to nature, "run back" to the wild state, the inference being that in nature the changes would not have been produced; and that the changes produced by cultivation are simply due to the abnormal conditions imposed upon plants. This objection, of course, is not a valid one, because man and nature are not likely to select the same variation, so that a variation selected by man is probably a very unfavorable variation in nature; in other words, a man-developed form would be an "unfit" form in nature. The very fact that nature changes an artificially developed form back to the favored structure in nature supports the theory rather than opposes it. It certainly indicates that a certain fitness for the conditions of living is necessary if an individual is to survive, and that this fitness can be developed by suppressing the more unfit in each generation.

Another objection advanced is that although a series of small variations may be piled up by continuous selection, securing what has been called a "cumulative effect," there is no evidence that such piling up can go on until the boundary of the species is crossed. In other words, there is a limit to such variations, and with all the variation that can be obtained in this way the resulting plants are still the same species. This objection has to do with fluctuating variations, which in the previous chapter were likened to the swinging of a pendulum. The range of the pendulum is greater in some species than in others, but it can never pass beyond a fixed limit. If this objection is a valid one, then it would seem hopeless to attempt to secure new forms by selecting among fluctuating variations. It must be remembered, however, that the limits of species are merely the expressions of varying human opinions. Just what constitutes a species is not much easier to define than evolution is to explain. What are called species are often connected by complete series of intergrading individuals, so that the species boundary is arbitrary. ''Species'' are freely broken up by investigators into two or more species; while in other cases two or more species are merged into one. In other words, a species is not a recognized unit with definite boundaries. To say, therefore, that artificial selection, and, by inference, natural selection, have never carried a variation across the species boundary is to talk of a limit that exists only as a convention.

It is the idea of ''adaptation'' that is associated with natural selection which has brought the most trouble. When this idea was first presented it was a captivating one, and great ingenuity was displayed in explaining the fitness of the forms that survived. For example, thorns were said to be established by selection, because their presence is a protection against grazing animals. It is known now that thorns prevail chiefly among plants in regions peculiarly free from grazing animals; and that, even if grazing animals are present, the thorns do not appear in the early stages of the plant, when they are most needed. Conversely, the plants chiefly attacked by grazing animals are singularly free from



Figs. 18 and 19.—Two plants of common gorse or furze (*Ulex*), showing the effect of environment: Fig. 18, a plant grown under moist conditions; Fig. 19, a plant grown under dry conditions, the leaves and branches having developed as thorns.—After Lothelier.

thorns. Experimental work has shown that thorns are merely responses to poor nutrition (Figs 18 and 19), and that they may or may not become an established character.

It is a well-known fact that many seeds, especially those of arid regions, develop a testa so hard that it interferes with the breaking through of the embryo; in fact, it is becoming evident that, if selection is working in these cases, it is working toward "over-adaptation." A striking case is that of the water-conducting vessels of plants which do not perform their very important function until the cells are dead (Fig. 20). Just how a group of dead cells performing a mechanical function could have been built up by natural selection is hard to imagine.

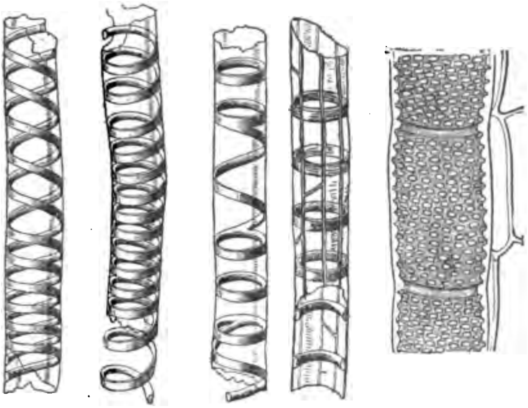


FIG. 20.—Water-conducting vessels.

Many such cases could be cited, and they are playing havoc with all the well-known "adaptations" of botanical literature. It must not be inferred, however, that such cases destroy all faith in natural selection, but they do tend to weaken faith. That there must be selection no one can deny, but when the selection includes unfavorable as well as favorable characters, it seems to have lost its motive. It seems evident that the selection of individuals holds no necessary relation to their useful characters. In short, natural selection simply means the destruction of certain individuals, and the preservation of others; and those that survive may be no better "adapted" than many that are destroyed.

The most fundamental objection to the theory of natural selection, however, is that it cannot originate characters; it only selects among characters already existing. If attention is restricted to some large genus, as *Aster*, the origin of its numerous species by natural selection seems a reasonable conclusion. The variations are endless and in every direction, and the intergrades are numerous. The genus has a definite group of characters and the species are simply varying expressions of these same characters. The pattern changes as in the kaleidoscope, but nothing new has entered into the combination. But when the genus boundary is crossed, and still more when the boundaries of the family are crossed, absolutely new characters are met on every hand, and yet relationship is still evident. In passing from one great group to another, evidently related to it by descent, but differing in the presence of new characters, one must raise the question, how could such characters have arisen by selection when as yet they did not exist? In other words, selection can only operate upon structures already present; to start an entirely new structure is not selection.

So far as plant-breeding is concerned, the conclusion to draw from these objections, so far as they are valid, is that artificial selection can increase any variations that exist, but that it cannot originate new forms. In other words, it may improve existing forms, but it cannot produce new ones. Furthermore, artificial selection may secure a variety of forms adapted to a variety of conditions, but it cannot deliberately adapt an unsuitable form so that it will become suitable; that is, it can increase the suitability of a form, but it cannot make it suitable.

SUMMARY

Darwin's theory of natural selection as an explanation of the origin of species is based upon the following facts: universal variation; the geometrical ratio of increase of living forms, resulting in severe competition (the "struggle for existence"), which destroys individuals less suited to the conditions of living, and spares those better suited; the striking results obtained with cultivated plants and domesticated animals by continuous selection (artificial selection), changes so great having been secured that often the wild originals cannot be recognized. From these facts the conclusion is drawn that a similar selection is going on in nature, the means of selection being the competition which follows from the ratio of increase and results in "the survival of the fittest."

The important objections are that the piling up of small variations by selection reaches a limit before the species boundary is crossed; that many unfit forms survive; and that selection cannot originate anything new.

The application of the theory and of the objections to it in plant-breeding is that forms can be improved by selection, but that they cannot be "adapted," and new forms cannot be produced.

CHAPTER III

THE THEORY OF MUTATION

A second theory of evolution that had a very direct effect on plant-breeding was published by DeVries, of Amsterdam, in 1901. The experimental work upon which this theory was based had a very important influence in putting the study of evolution upon an experimental basis, which may be regarded as the modern period in the history of evolution. During this period students of evolution ceased to be interested in the speculative genealogies of plants, because such genealogies could not be demonstrated. They confined themselves to an extensive investigation of the problem of how one species arises from another. If this can be demonstrated, the explanation of evolution will be secured, and just how the various great groups of plants have arisen is of relatively small importance, because it is beyond the reach of experiment. In the origin of individuals, for example, the fact that one individual arises from another is the important fact, even if it is impossible to trace the exact ancestry of every individual. DeVries was conspicuous among those who introduced experimental methods for the study of evolution, thus narrowing the study to the region of possible demonstration.

More than a quarter of a century ago DeVries discovered an American evening primrose (*Oenothera Lamarckiana*) in a waste field in Holland, where it had been introduced and was multiplying rapidly (Fig. 21). In association with it were certain unknown and very distinct forms, the association suggesting that they had been derived from the normal *O. Lamarckiana.* Seeds were secured from the normal plants, and cultures were begun in the Botanical Garden of the University of Amsterdam, and from the first sowing another form was obtained. Then DeVries began a long series of pedigree cultures, and continued them through several generations before announcing his theory. Quite a number of distinct forms were secured from *O. Lamarckiana,* appearing among the ordinary progeny in about the proportion of 1.5 per cent. (Figs. 22 and 23). Some of these varying forms appeared repeatedly, some appeared only once, and upon subjecting them to pedigree culture they bred true to their characters. The conclusion was that the new forms arose suddenly, without any intermediate forms, and remained distinct from the parent plant. These suddenly appearing and constant forms proved to be good species, that is, they had the characters that had been used in distinguishing species of *Oenothera.* Moreover, they were species that had never been described before, and have never been found

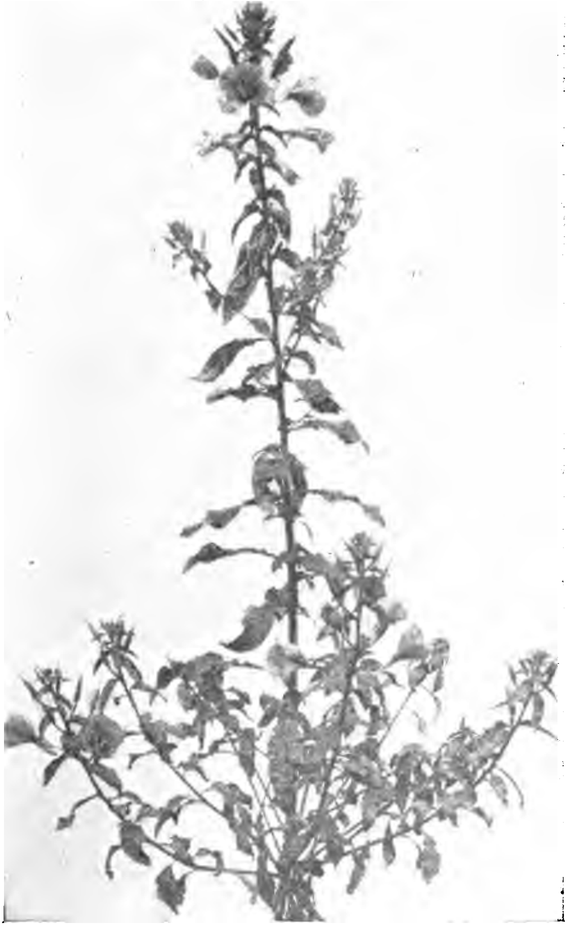


FIG. 21.—Lamarck's evening primrose (*Oenothera Lamarckiana*).—After DEVRIES.

wild since, so that if *O. Lamarckiana* had been "throwing them off," they had not survived in nature. These new species were fully equipped species from the start, coming from the parent form "in a single bound," and were not built up through generations by a slow accumulation of small variations. This kind of variation was called a *mutation,* and DeVries concluded that species arise from other species in this way. Of course such extreme variations had been noted, and were commonly called "sports," but no particular significance had been attached to them.

The notable difference, however, between these variations and the ordinary fluctuating variations was not so much the amount of the variation as its constancy, and it is constancy that is used as the test of a species. If species originate by such sudden jumps, DeVries points out that the rôle of natural selection is not to produce new species, but to select among those already produced. In other words, these "mutants" occur in every direction, and many of them are not equipped to continue in the conditions of nature; so that many disappear, and some survive, which of course is a natural selection of species.

If new species are produced by mutations, rather than by the slow, cumulative effects of natural selection, it becomes necessary to explain the extensive changes effected by artificial selection. It will be remembered that Darwin used the long experience of man with arti-

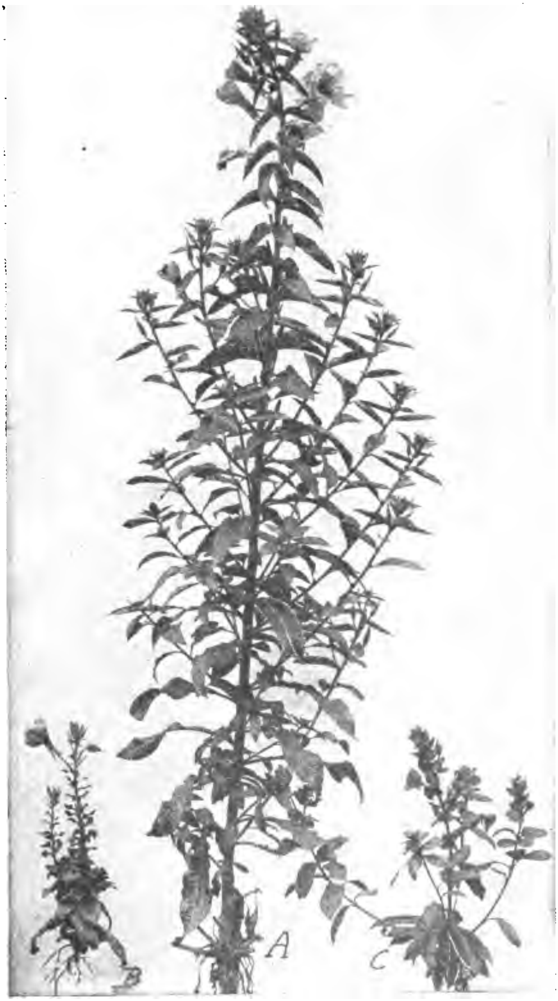


FIG. 22.—Mutants from *Oenothera Lamarckiana: A,* the red-veined form (*O. rubrinervis*) ; *B* and *C,* the dwarf form (*O, nanella*).—After DEVRIES.

ficial selection to support his claim that a similar process in nature produces new species. The common view was that artificial selection results in large changes by piling up small, fluctuating variations generation after generation. In fact, such slow, cumulative changes are matters of definite experience in the cultivation of plants, resulting in "improvements," as they may be called. Improved races, produced by artificial selection through a succession of generations, are being announced every year.

In examining all the available records of the experiences of plant-breeders, DeVries could find no evidence that the so-called "improvements" ever stood for new species, since they did not stand the fundamental test of constancy. The "improvements" did not persist except by continued selection, and the changes induced, therefore, were fluctuating variations rather than fixed changes. In searching through the vast number of changes in plants brought about by the operations of man, DeVries was able to find a few that seemed to be really new things, as indicated by their constancy. In examining the history of these new things, so far as it was available, he found that they were not produced by long-continued selection, but appeared suddenly as solitary individuals, with established characters, and sometimes new characters, that bred true generation after generation. In other words, they had appeared as mutants rather than as the result of artificial selection.

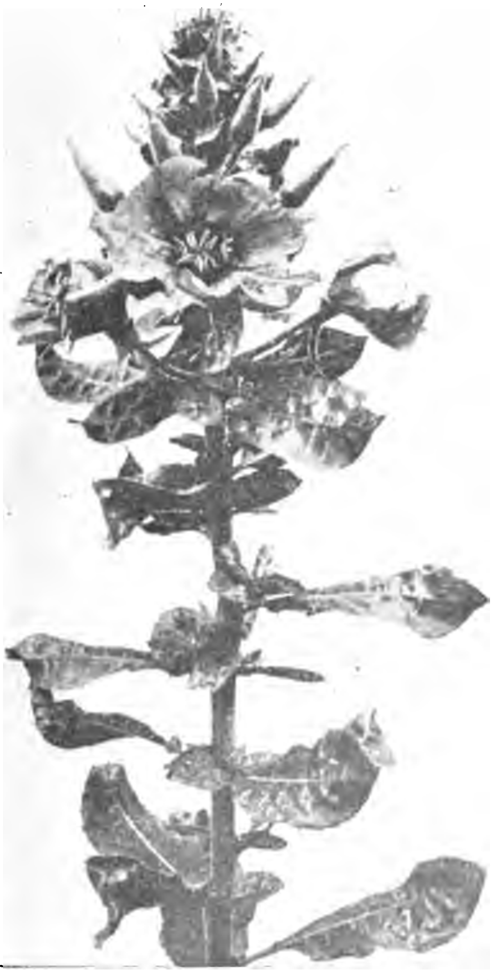


FIG. 23.—A flower spike of the giant mutant (*O. gigas*).—After DE VRIES.

If the conclusions of DeVries are to be accepted, therefore, the breeding of plants by artificial selection resulted generally in "improvements," which are not constant; and occasionally "mutants" appear, which are constant, and therefore answer the test of new species. For example, in Burbank's cultures of dahlias there appeared a single individual with lavender fragrance, so noticeable, in fact, that the fragrance was detected before it was associated with the plant. This unusual quality for a dahlia had never been known before, and if it had been left to be mixed with ordinary dahlias it would probably have disappeared. But this individual was pedigreed, the unique character reappeared in all of its progeny, and in this way a race of lavender-scented dahlias was established. This character is, of course, a physiological one, but it proved to be associated with morphological differences also, so that this suddenly appearing new race was distinct, had not been built up gradually by selection, and remained constant.

The application of the theory of mutation to practical plant-breeding became at once apparent. It might be used in securing in great numbers desirable new forms which had appeared so rarely in connection with artificial selection, and then, not because of it. The method suggested would be an indefinite multiplication of individuals, and then a search among them for new and desirable forms. In other words, new forms need not be produced, but found. Inferentially, variation is so constant and diverse that any form desired might occur, if only individuals enough were secured. Another practical advantage suggested was constancy. Merely improved races never remained constant except by continuous selection. When they came into the hands of the farmer, for example, who could not be expected to continue the careful selection practiced by the professional plant-breeder, they began to deteriorate, season after season, so that the farmer was compelled to secure new supplies of "guarded stock." While this worked to the advantage of the seedsmen, it was a handicap to the farmer. A scheme, therefore, which could secure numerous new forms rapidly, and at the same time insure their constancy, was a great simplification of the problems of practical plant-breeding. It remained, however, to prove that mutations are general, and can be depended upon to supply all the desirable variations that the cultivation of plants demands.

The announcement of the theory of mutation naturally raised the question whether all plants are producing mutants, or whether this phenomenon is peculiar to the evening primrose studied by DeVries. That other plants have produced mutants occasionally in cultivation seems to have been shown, but is the mutating condition found among wild plants in general? Since the recognition of mutants requires generations of breeding, the search for mutating plants has advanced slowly, but quite a number have been found. For example, the very common "shepherd's purse" is evidently mutating just as freely as is the evening primrose. The appearance of a mutant in 1912 in a field of tobacco is interesting. On a Connecticut tobacco plantation, in a field including about one hundred acres, one plant was observed very much taller than the others, with more leaves, and with other distinguishing characters. A careful search discovered two other such plants. From one of these plants, removed to the Connecticut Agricultural Experiment Station, 5,000 seedlings were obtained. They remained true to type. This suddenly appearing type answers thus far all the tests of a mutant that can be applied in so short a time.

On the other hand, many plants have been tested with negative results, no evidence of mutations being obtained. It seemed obvious to DeVries that many plants are not in a "mutating condition," and that probably mutating plants are not in this condition all the time. For example, *O. Lamarckiana* is a native of the United States, but it seems to have disappeared completely from our flora, for it has been searched for diligently. The evidence seems clear that a century or more ago it was a constituent of the flora of our Atlantic seaboard. If it were mutating then as freely as it is now, wherever it is under cultivation, it would be expected that some of its mutants would remain as members of our flora, or, at least, that they would have been discovered and described as *O. Lamarckiana* was, but the mutants that have come from this form repeatedly under cultivation are forms that have never been seen in nature. For this reason DeVries concluded that the mutating condition represents a particular period in the history of a plant, so that plants in this condition now may cease to produce mutants presently, and plants not in this condition now may produce mutants later. Of course, this is merely a speculation without any knowledge as to the meaning of the "mutating condition," but it is one method of stating that mutation is not a universal or constant phenomenon.

The behavior of *O. Lamarckiana* suggested to DeVries one of two alternative conclusions: either this plant was producing new species (mutants), or it was a hybrid that was splitting up into the different species that had combined to produce it. To settle this question, DeVries sought to discover a test for a hybrid, and in so doing discovered the work of Mendel, which had been lost to the world for many years. Mendel was an Austrian monk who had worked with hybrids, and had discovered a law of inheritance that is now called by his name. "Mendel's law" will be considered in another chapter, but, at this point, it may be said that it may be used as a test for hybrids. For example, a hybrid plant "splits up" in its progeny in a certain definite proportion; a certain number of the progeny resembling one parent, a certain number resembling the other parent, and the remainder retaining the mixed characters of both parents. Upon applying this test to his evening primrose, DeVries concluded that it did not act like a hybrid, for the new forms it produced were far too few to represent the ratio of a splitting hybrid. For example, approximately 50 per cent. of the progeny of a hybrid should resemble one parent or the other; while the new forms produced by the evening primrose averaged only about 1.5 per cent. of the progeny. DeVries concluded, therefore, that he was dealing with a "pure strain" and not with a hybrid. He realized, of course, that many so-called "species" in nature are hybrid mixtures, and that pure strains can be secured only by continuous and guarded pedigree culture. If a pure strain can "throw off" new species, then mutation certainly becomes a method of evolution. The exact definition of a mutant, therefore, is a new species produced in a single generation by a pure strain. Since most plants seem to be mixtures of varying complexity, a pure strain can only be recognized by rigid pedigree culture. To call plants mutants, therefore, on the basis of inspection, is entirely untrustworthy.

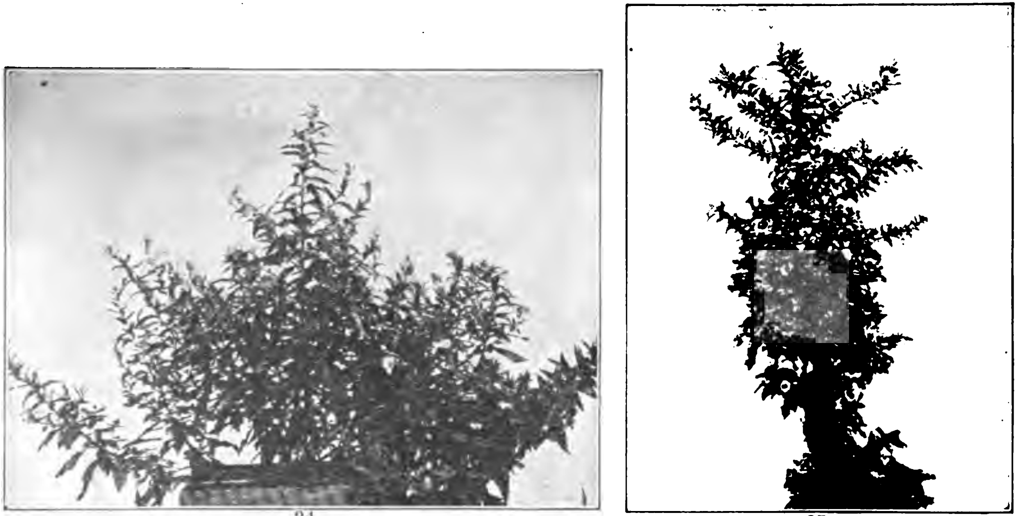
Those who are opposed to the theory of mutation claim that *O. Lamarckiana* is a hybrid mixture, and that the "mutants" are simply the products of a splitting hybrid which do not follow the Mendelian ratio. Much experimental work has been done in attempting to prove this claim, the difficulty of the proof lying chiefly in the fact that *O. Lamarckiana* has disappeared as a wild plant and is known only as an introduced plant and in cultivation. Of course, the theory of mutation is still on trial, for the time has been far too short to test it. Naturally it has been accepted with great enthusiasm by some as settling the method of evolution; on the other hand, it has been rejected as positively by others. In neither case is the opinion based upon adequate evidence, and, in all probability, the truth lies somewhere between the two extreme views. When two groups of competent men are at opposite extremes of opinion they are stimulated to make extreme claims, and the truth is probably somewhere in the neutral ground between them.

No one doubts the facts reported by DeVries in reference to his evening primrose, or the conclusion that his "mutants" are good species. But it is still allowable to ask two questions. Is mutation a phenomenon of plants and animals in general, or, is it only an exceptional phenomenon? If it is true in general, then possibly new species in general appear as mutants. If it is an exceptional phenomenon, then new species may appear occasionally as mutants. In other words, the answer to this question will determine whether mutation is a rule or an exception. The other question is, are mutants *new* species, even if they are *good* species? May they not be old species disentangled from a hybrid mixture? Mendel's law seems to answer this question in the negative, but is Mendel's law infallible? There are facts accumulating which seem to indicate that it is not.

In all probability, mutation is one way in which new species have appeared; and natural selection may be another way; and in addition to these there are probably other ways. In other words, we can hardly expect to find a solitary method for evolution; to explain it we will probably need all of the explanations that have been offered and many more besides.

Whether mutation stands as a general explanation of evolution or not, the work of DeVries opened up a method that has proved of immense service in the practical cultivation of plants.

There has been some attempt to discover the cause of mutation. It seems obvious that it results from some change in the "germ plasm"—that is, the living substance of the sexual cells. Some experiments have indicated that any "disturbance" of the germ plasm, which means an abnormal condition, may result in a mutant (Figs. 24 and 25). If this is true, mutation does not depend upon a particular period in the history of a plant, but may occur at any time if the germ plasm is altered. In other words, it is dependent, not



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Figs. 24 and 25.—Two plants of *Oenothera biennis*, showing the effect of injections of zinc sulphate into the ovule: Fig. 24, the normal plant; Fig. 25, the modified plant, raised from seeds developed by injected ovules.—After MacDougal.

upon a period, but upon a condition. This suggests that it is not too much to expect that at some time when the conditions that favor mutation are known and under control, mutations may be multiplied artificially and desirable new forms secured in this way.

SUMMARY

The theory of mutation as an explanation of the origin of species was based upon the experimental study of *Oenothera Lamarckiana* (evening primrose) through many generations. During this experimental work it was observed to give off a variety of new forms in every generation in very small proportion to the total progeny. These new forms proved to be good species, not merely in their superficial characters, but chiefly in their constancy, showing no tendency to "run back" to the parent stock.

This mutating condition has been observed in other plants and in animals, but since its recognition requires carefully guarded cultures through several generations, the extent to which it occurs in nature is unknown.

The argument against mutation is that mutating plants are hybrids, and therefore the appearance of "mutants" is the splitting of a hybrid. It would follow that the forms that are thrown off in a single generation do not represent the appearance of new species but the reappearance of old ones that have formed the hybrid mixture.

THE THEORY OF MUTATION.

The practical application of the theory of mutation to plant-breeding is that it suggests a method of securing new and constant forms, as contrasted with the inconstant improvements of the old method of artificial selection.

CHAPTER IV

SOME SUPPLEMENTARY THEORIES

There are certain other theories of evolution which deserve brief mention. They are not so definitely associated with authors and have not been developed so fully and independently as are the theories of natural selection and mutation, but they must be included in any consideration of organic evolution.

The theory of *orthogenesis* is coming to be a prominent one and is being supported by an increasing number of investigators. Probably the first adequate statement of the conception was made by Naegeli in 1883, then Professor of Botany at Munich, who called it "progressive evolution." Naegeli insisted that each species is compelled by some internal cause, something in its constitution, to develop into new forms independent of environment and independent of any struggle for existence. Like a train upon a track, there is progress in a given direction; that is, there is persistent variation in certain definite and predetermined lines, a kind of variation that has been called "determinate variation," as contrasted with ordinary "indeterminate variation." The probability of orthogenesis becomes impressive when one turns from closely related species, and considers how great groups have arisen from one another. For example, in such a group as Gymnosperms there is material available for study representing a tremendous stretch of history, at least from the middle Paleozoic to the present time. Through all this stretch of history, in spite of all imaginable changes in external conditions, certain structures have changed steadily in one direction. A few illustrations will make this situation concrete.

Gymnosperms seem to be about the least plastic of the great groups of land plants. There is among them little or no visible response in nature to changing conditions of the most extreme kinds. It would seem that selection among these relatively invariable forms can hardly be more than the accident of crowding. Certainly, one can lay hold of no kind of variation in nature that even suggests the coming characters of another species, much less of another genus or family. And yet, the group as a whole shows that certain distinct evolutionary tendencies have been worked out in a progressive way.

For example, the plant which produces the female sex organs, known as the female gametophyte, is not only in the midst of an ovule invested by a thick integument, but it is also directly inclosed by the heavy wall of the spore that produced it. If any structure is shut away from the influences of a changing environment, it would seem to be this one. And yet, through the whole series of Gymnosperms, this gametophyte shows a progressive transformation. In the more primitive forms it matures as a relatively large mass of tissue, and late in its history the female sex organs appear. In the first stage of its development it consists of a large number of free nuclei; in the second stage walls appear and a tissue is formed; and in the last stage this tissue grows and finally produces the sex organs with their eggs. The constant tendency throughout the whole group is to produce the sex organs earlier and earlier in the history of the gametophyte. A series can be arranged illustrating the appearance of the sex organs at what might be called the mature stage of the gametophyte at one extreme; then their appearance at earlier and earlier stages of the tissue development, until they appear with the first formation of walls; and finally, at the other extreme, the eggs appear at the stage of free nuclei. This progressive slipping back of the egg in the development of the gametophyte holds no relation to any change in fertilization, for that is a prolonged process among Gymnosperms. Taking the group as a whole, this is not a sporadic change, occurring here and there, but the two extremes given are the two extremes of the Gymnosperm line. This kind of progressive change is beyond the reach of experiment, and its explanation is beyond the reach of imagination as yet.

The same kind of progressive change is shown in the embryo of Gymnosperms. In the most primitive condition the first stage of embryo formation is extensive, free nuclear division, the nuclei being distributed through the fertilized egg; after this walls are formed and the egg becomes filled with tissue called the proembryo (Fig. 26). Throughout the Gymnosperm series there is a steady reduction in the number of free nuclear divisions, and with it a reduction in the amount of proembryonic tissue, so that finally this tissue occupies a very small part of the fertilized egg (Fig. 27). All this change has taken place further from outside influences than the change in the gametophyte, for the embryo is imbedded in the gametophyte.

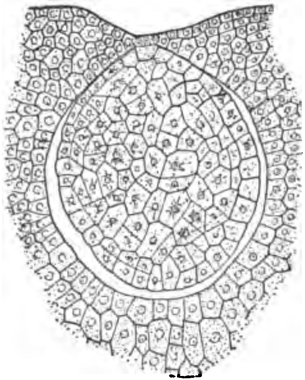

FIG. 26.—Proembryo of *Ginkgo*, filling the egg with tissue.—After STRASBURGER. From Coulter, Barnes and Cowles' "Textbook of Botany."

It may be claimed that these are not the characters that students of classification use in distinguishing species. This is true, but they are just the characters that distinguish great groups, and represent the advancement of the plant kingdom as a whole. It so happens that both the progressive changes noted above as occurring among Gymnosperms culminate among Angiosperms. They represent, therefore, progressive changes occurring steadily throughout the history of seed plants. It may be said that in such cases we are dealing with structures that have ceased to be useful, and therefore are being gradually eliminated. No one can say how useful they are, but no one can deny that they are functional.

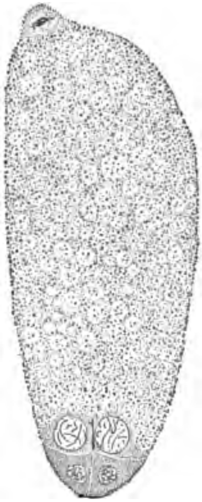

FIG. 27. — Proembryo of a pine, comprising a few cells at one end of the egg.—From Coulter, Barnes and Cowles' "Textbook of Botany."

Natural selection, mutation, and orthogenesis are not mutually exclusive theories, since they all deal with variations. Natural selection deals with fluctuating variations, usually small, and in every direction. Mutation deals with constant variations, usually large, and in every direction. Orthogenesis deals with small or large variations, which for some reason persist and increase from generation to generation, carrying forward the group as a whole. It is one thing to pass from species to species within the limits of a small natural group, and a very different thing to pass from one great group to another. The characters of a genus may have been juggled in a variety of ways to form what we call species, and among these ways may have been both natural selection and mutation; but this only secures the final diversity of species.

Behind species are the great groups with different characters, and any study of a long history shows that such differences have been wrought out by steady and progressive changes through all imaginable changes of environment. Species have been likened to the individual waves that appear on the surface of a choppy sea; if so, the deep-seated changes brought about by orthogenesis, and which history makes so evident, may be likened to the great oceanic currents, whose movement and direction proceed with no relation to the choppy surface.

Another conspicuous factor in evolution, and one that has been claimed as a cause of evolution, is *isolation*. As individuals are multiplied they spread over a wider geographical range, and as a result a group of individuals may become separated from the main group by some barrier. This barrier may be a literal one, as a lofty mountain range or an extensive body of water, or in the case of plants it may be simply a belt of country that for some reason cannot be occupied. In any event, the isolated group of individuals is prevented from interbreeding with the rest of their kind. As a consequence, any peculiarity of the detached group would become intensified, until eventually they would become quite distinct from the main assemblage of individuals. The study of the geographical distribution of plants and animals has been the basis for this view. Besides geographical isolation, there may be developed a physiological isolation, certain individuals appearing that for some reason cannot mate freely with others of the general group. Isolation as a factor in evolution has been studied most intensively and successfully among fishes, and the results have been very striking.

In analyzing the results of isolation, however, it becomes evident that it does not induce variations, but may give certain variations a chance to continue. In a large population individual variations are swamped by interbreeding, the whole population representing an average of the variations of individuals; but if an individual be isolated from its kind any peculiar variation it possesses may become intensified. In this way an isolated group of individuals may become so different from the group from which it has become detached as to deserve recognition as a distinct variety or species. In short, isolation does not produce species, but gives them a chance to develop; it is not origin, but opportunity. In other words, it is a form of natural selection; ordinarily selection is secured by competition, but in this case it is secured by isolation.

It was inevitable that students of evolution should speculate in reference to the machinery of heredity. They observed an unbroken succession of similar forms in a given pedigree, so similar that they resemble one another more than they do any other forms. An egg produces a body resembling that of the parent more closely than that of any other species. It was natural to ask the question, what determines that a given egg shall produce one kind of body rather than another? To understand how new species sometimes arise from old ones it is necessary to understand how new forms usually do *not* arise from old ones, but the same kind of individuals appear through endless generations. Before heredity became an experimental study it was natural that speculation should suggest explanations of the transmission of essential similarity, and also of the relatively slight modifications that define individuality. Some of these speculations are of interest because of their influence upon current opinion, or because of their influence upon investigation.

The earliest speculation concerning heredity seems very natural, and therefore inevitable. It was thought that a given egg is restricted to the production of a certain kind of body, because all the parts of that body exist in miniature in the egg. It was not very long ago that it was common to hear that an acorn contains an oak tree in miniature, and that a sufficiently powerful microscope might be able to reveal it. An acorn is not an egg, but it serves as an illustration of this conception of an egg, namely, that it contains all the parts of the body already formed. This is called the doctrine of *preformation,* and it held sway most persistently. If a given egg produced an animal with wings, there seemed no other explanation than that wings existed already formed in the egg, and only needed to grow, and so for every organ of every body. This gross conception of heredity, of course, did not stand the test of scientific analysis, but the doctrine in more refined form appears in later speculations. Perhaps the most famous of these is Darwin's theory of *pangenesis,* proposed in 1888.

Darwin realized that the gross form of the doctrine of preformation was untenable, and therefore proposed a theory of heredity based upon the conception of invisible particles, "biological atoms," they may be called. These exceedingly minute material particles he called *gemmules,* and their function in heredity was to transmit the characters of the parent to the offspring. He conceived that every cell of the body produces and throws off its gemmules, which multiply indefinitely. These gemmules find their way to the reproductive cells; in animals by the blood stream, in plants by no such obvious method. Thus they collect in the reproductive cells, each one of which comes to contain gemmules representing every part of the body, in fact, every cell of the body. His picture of a plant or animal body, therefore, is of these biological atoms swarming from everywhere into the reproductive cells. When a fertilized egg produces a new individual, each gemmule it contains causes a duplication of the part from which it came in the parent body. Since every cell of the parent body is represented in the egg by gemmules, every part of the parent body will be duplicated in the progeny. Since all of the cells of the parent body are concerned in heredity, the doctrine was called "pangenesis." It certainly would involve the inheritance of acquired characters to the last detail. For example, it would be hard to understand, according to this doctrine, how a parent with an amputated arm could transmit two arms. But this conception seemed to Darwin the only method of accounting for the wonderfully detailed duplication that appears in inheritance. This view is really a very refined preformation, for fundamentally it means that every part of the parent body is represented in the egg, if not in actual form, at least by material particles that only need to grow or to determine growth.

The same conception appears in the "pangenes" of DeVries, which are Darwin's gemmules, and in the more ancient "chains of micellæ" of Naegeli. In all cases, by some mechanism, every part of the body influences the reproductive cells in such a way as to determine to the last detail the kind of body an egg will produce.

Perhaps the most influential speculation in reference to the machinery of heredity was that of Weismann, a German zoölogist of Freiberg, who in 1892 proposed his theory of *the continuity of the germ plasm.* It was certainly a direct contradiction of the doctrine of preformation and all of its refinements. As a corollary it undertook to prove that acquired characters are not inherited, a view which controverted a very general belief. An "acquired character" needs strict definition, or its use by Weismann will be misunderstood. It is a character that an individual has not inherited, but has acquired in the course of its own lifetime, as, for example, a scar, some muscle development, or any body feature. Furthermore, the character thus acquired must have no influence upon the reproductive cells, but must be confined to the body (somatic) cells, or else it will affect inheritance. In other words, an acquired character in the Weismannian sense is one that is taken on during the life of the individual, and is not transmitted to its progeny.

The argument presented by Weismann was so clear and convincing that it made a great impression and has been very influential in stimulating research. In outline it is as follows.[1] It has become a matter of observation that the egg does not contain any trace of the series of organs it will produce. When it divides it starts a series of cell generations that presently become different kinds of cells, and these eventually enter into the structure of the various organs of the completed body. Weismann claims that among all the kinds of cells that arise in connection with the forming body the reproductive cells are the least modified from the original condition; that is, the reproductive cells are more nearly like the egg from which all the cells have descended than are any other cells. Every organ of the body traces its cell lineage back to the egg, and each organ has its own lineage distinct from the others. As the histories of the different organs are retraced toward the egg, they converge, the common starting point for two neighboring organs being reached sooner than for two widely separated organs. Finally all the histories come together in the egg. It follows that reproductive cells have a history of their own, and the direct line of cell generations from the parental egg to the reproductive cells is distinct from the lines leading to the other organs of the body. The reproductive cells are the only ones concerned in reproducing offspring, and therefore the cell lineage leading to the reproductive cells is the only one continued into another generation. All the other cell lineages terminate with the death of the organs in which they have entered. It follows that a series of similar individuals appearing generation after generation is determined only by the series of cells leading to the reproductive cells; all the other cell lineages lead to offshoots that perish. Therefore, a child inherits from the reproductive cell of the parent, and not from the body of the parent; and the reproductive cell owes its character, not to the body which contains it, but to its descent from previous reproductive cells. The conclusion is reached, therefore, that the body, so far as reproduction is concerned, is merely a carrier or container of the reproductive cells, ''which are held in trust for coming generations.'' It follows that a character acquired by the body, after it has been formed, and therefore a character that has no connection with the series of cells extending from the egg to the reproductive cells, has no chance to be passed on to another generation. This unbroken chain of cells that runs from egg to reproductive cell, and so on into subsequent generations, is what Weismann calls "the continuity of the germ plasm," as distinct from the discontinuity of the body plasm, which comes to an end with each generation.

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[1] An excellent brief statement of Weismann's theory is given by Lock in his "Recent Progress in the Study of Variation, Heredity, and Evolution" (1906). The substance of this statement is used in the above outline.

Weismann also constructed an elaborate hypothetical mechanism for heredity. His "architecture of the germ cell" is a noteworthy piece of imaginative work which has been somewhat confirmed in a general way by the later work in cytology and genetics. He called the hereditary substance which is characteristic of the reproductive cells and their cell lineage *germ plasm.* This he conceived of as consisting of a variable number of *idants,* which represent the gross units of structure of the germ plasm. These idants are suggestive of the chromosomes, which later came to be regarded as the visible carriers of heredity. The idants in turn are made up of *ids,* which may be thought of as "biological molecules," while each id is composed of *biophores,* which are the smallest conceivable particles of germ plasm, and may be called "biological atoms." Each biophore plays a definite rôle in heredity, and is suggestive of the "determiner" of geneticists. The conception of a system of biophores constituting an id; and a system of ids constituting an idant; and a system of idants constituting the germ plasm of a reproductive cell, certainly furnished enough machinery for all the results of reproduction. Since every part of the body that is to be produced is represented by a biophore, this conception is the same as Darwin's pangenesis, but differs from it fundamentally in restricting its application to the reproductive cells and their cell lineage.

Of course Weismann had to account for variation, and this he does by the mingling of two collections of biophores in the sex act. This he calls *amphimixis,* or blending, and conceives of this mixture of biophores from two sources as engaging in a struggle for existence. The selection of biophores which results from this struggle determines the character of the individual that the egg will produce. This is "intra-selection," or internal selection, as contrasted with Darwin's natural selection, which is external selection, that is, a selection made by conditions outside the body. Weismann regarded external conditions, not as developing characters, but as stimulating to development characters already represented in the germ cells by biophores. In other words, external conditions are not the causes of characters, but the conditions for their appearance.

It is remarkable how much of this conception may be regarded as a general prophecy of what later investigation discovered. In its broad outline it touched upon the most conspicuous findings of cytology and genetics, either in fact or in idea. Weismannism as an influential theory of heredity was replaced by Mendelism, which is now the dominating influence in genetics, but Weismann's conception marked a distinct advance in the study of heredity, for it emphasized the fact that the reproductive cells are more or less isolated from the influence of the body cells, and it called attention to the chromosomes as the structures of the nucleus chiefly concerned with heredity.

The striking contrast between the theory of Weismann and the results of Mendel is in the contribution of each parent to the offspring. Weismann thought that all the characters of both parents are represented by ids in the fertilized egg. This was the necessary antecedent to "amphimixis." Mendel, on the other hand, showed that characters are segregated in the reproductive cells. Of two contrasting characters of the parents only one of them is represented in the reproductive cell of the child. In other words, a reproductive cell does not contain all the ancestral characters, but each character is from one of the parents, to the complete exclusion of the other. A reproductive cell, therefore, contains a selection of characters from its ancestry, and not a complete collection. All of the characters of an individual zigzag through one side of the house in each generation. This situation, however, could hardly have been imagined before any experimental work could have proved it, for it seemed most natural to assume that both parents contribute all of their characters to the child.

One of the first claims of Weismann to be tested by experimental work was the claim that acquired characters are not inherited. A striking experiment was the transplanting of the ovaries of guinea pigs by Castle. Ovaries were removed from the body of a young animal and allowed to mature in the body of a different kind of guinea pig. The reproductive cells in these ovaries were thus subjected to the influence of a great variation in the body. If the body cells ever transmit their characters to the reproductive cells it should become obvious in such a case. But there was no result. The reproductive cells from these transplanted ovaries produced individuals like those from which the young ovaries had been obtained. In other words, the characters had come from the egg that produced the first body, and not from the body that had brought the ovary to maturity. The conclusion is that the body is simply a nurse for the reproductive cells, and that it no more determines the kind of body that will be produced than does food. The experiments of Tower with potato beetles show the same result. He subjected beetles through many generations to varying conditions of temperature, humidity, light, etc., and obtained all sorts of colors and color patterns as responses. These are obviously purely body characters. These induced characters, however, which are clearly acquired characters, had no influence whatsoever on the colors of succeeding generations.

Even before such experimental results had been obtained it is surprising that there was such a persistent belief that acquired characters are inherited. Attention had long been called to the fact that certain savage races, generation after generation, induce monstrous developments of ears, nose, and lips, and yet such acquired characters are never inherited. The binding of the feet of Chinese women was practiced for centuries, and still the results of the binding were never inherited. The inference is that in order to secure new forms the germ plasm must be modified. How this is done in nature is under consideration; that it can be done experimentally has been demonstrated (Figs. 24 and 25). The various theories of evolution and heredity have suggested that this modification of the germ plasm, resulting in changed forms, is brought about by changes in environment, by selection, by amphimixis, by hybridizing, by orthogenesis, etc. Some of these claims have been disproved, and the others remain in doubt. In any event, the history of the subject is a good illustration of the usual method of progress in science. The first stage is a series of shrewd speculations, founded upon general observations; this is followed by more detailed observations that reject certain speculations and show that others are worth following up; and, finally, rigid experimental work begins to establish a body of facts, gradually dissipating some speculations and transforming others into facts. The study of heredity at present has begun a development of this last stage. Certain facts have been established, but much speculation remains as yet to be tested.

SUMMARY

An important theory of evolution is orthogenesis, which means that progressive changes occur in organisms in a definite direction, uninfluenced by changes in environment, and apparently due to causes within the organism itself. This theory accounts for the evolution of great groups, while natural selection and mutation may explain the origin of species.

Isolation has also been regarded as a factor in evolution, by which is meant that the separation of a group of individuals from the general mass of their relatives, so that they cannot interbreed, may result in a distinct variety or species. This separation simply permits individual peculiarities to be perpetuated and increased, and therefore isolation does not produce a new species, but permits one to develop. In other words, it is one form of natural selection, the usual form being competition.

Studies of evolution early led to speculations concerning the machinery of heredity. The earliest was the doctrine of preformation, which means that all parts of the body exist in miniature in the egg, and only need to grow. Later, Darwin's theory of pangenesis proposed invisible particles (gemmules) as being produced by every cell of the body, collecting in the egg, and determining in detail the kind of body it produces.

The most notable speculation concerning the machinery of heredity was that of Weismann, who proposed the theory of continuity of the germ plasm, meaning that the germ plasm and the body plasm are distinctly differentiated; that the germ plasm is continuous through all the cell generations, from the parental egg to the reproductive cells of the next generation, and so on into the generations that follow; while the history of the body plasm ends each generation with the disappearance of the body structures. This implies that acquired characters are not inherited; that is, characters that are taken on by an individual in its lifetime, and that have not come from the egg. In imagining the "architecture" of the germ plasm, with its idants, ids, and biophores, Weismann forecast in a general way the later discoveries of cytology and genetics.

The bearing of these speculations and theories on plant-breeding is found chiefly in the question of the inheritance of acquired characters. If acquired characters are not inherited, then any modification of a plant dependent upon its environment is not necessarily inherited if the environment is changed. If some acquired characters can be inherited, then these can be passed on, even if the environment does change. In any event, it must be recognized that if acquired characters, through their effect on nutrition or otherwise, affect the reproductive cells, then they must influence inheritance. According to Weismann's definition, therefore, one can only tell through inheritance whether an acquired character has affected the reproductive cells or not.

CHAPTER V

REPRODUCTION

In intelligent plant-breeding nothing is more essential than some knowledge of the different kinds of reproduction and their significance. Familiarity with reproduction in the higher animals and man has given the impression that all reproduction necessarily involves sex, and that the significance of sex is reproduction. This mistaken idea is responsible for much crude teaching in reference to plant-breeding. The universal occurrence of asexual reproduction among plants is not generally appreciated. There is no question that many more plants are produced asexually than sexually. This makes it clear that sex is not an essential feature of reproduction, and that the significance of sex is not to secure reproduction, but to secure something in connection with it that other methods of reproduction do not. Although in man and the higher animals the sex method has become the only method of reproduction, among plants asexual reproduction is not even a declining method. In plants also the origin of the sexual method is in evidence, so that the conditions of its appearance are clear, and its significance becomes apparent.

REPRODUCTION

It will lead to a better understanding of reproduction if the three methods exhibited by plants are considered in the order of their appearance. It should be understood that the word "reproduction" will be used in the ordinary sense; that is, meaning the production of a new individual. This explanation is necessary, for in a very real sense any cell division resulting in the production of two new cells is reproduction, but the result may not be a new individual, but only growth of the body, or restoration of wasted tissue, or healing a wound.

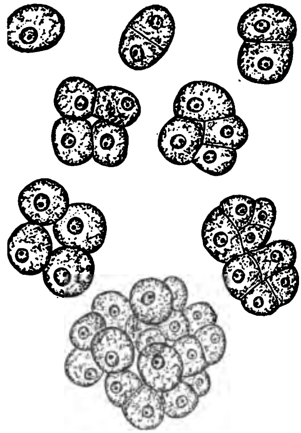


Fig. 28.—Vegetative multiplication of a one-celled alga (*Pleurococcus*) : in the upper left-hand corner is a single plant (one cell) ; in the other figures the cell has divided and given rise to loose groups of individuals.

The first method of reproduction among plants is cell division. A one-celled individual divides and produces two new individuals (Fig. 28). The individual in this case is a single protoplast; that is, the organized living substance (protoplasm) of a cell. This self-division of a protoplast is one of its powers, and the elaborate machinery of cell division has secured an exactly equal division of all the structures of the protoplast, so that the two new cells (individuals) are duplicates of the parent cell. The fundamental reproductive mechanism, therefore, is cell division, whether the method is sexual or asexual. In the sexual method a fusion of cells precedes cell division, and this fusion is evidently an added preliminary process, not essential to reproduction, but securing something in connection with it. The power of self-division, therefore, which is the essential process of reproduction, is a function of every protoplast, which may be permitted or inhibited by varying conditions. In one-celled plants the cell wall is involved in this division, but the wall is an incident that may be eliminated. This division of ordinary vegetative cells to produce new individuals is called *vegetative multiplication,* and it is a method used by all plants. Even among the seed plants vegetative multiplication is very common, and use is made of it in

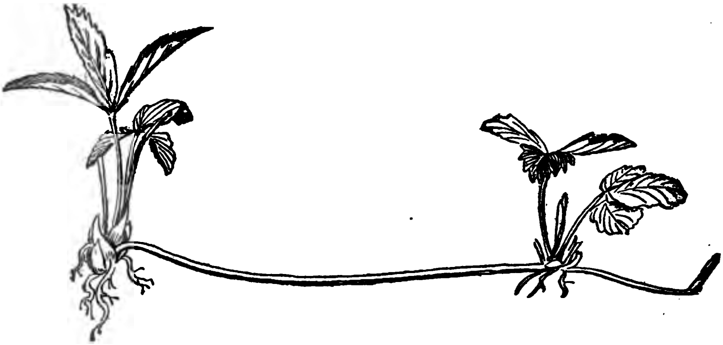


FIG. 29.—A strawberry plant, showing a runner that has developed a new plant.—After SEUBERT.

securing new individuals from bulbs, tubers, cuttings, runners (Fig. 29), etc., which are parts of the vegetative body.

A further statement concerning the power of vegetative multiplication exhibited by seed plants may make the situation clearer. The stem, for example, is not a uniform structure throughout, but is differentiated into nodes and internodes, each with its own functions. The nodes give rise to the lateral appendages (leaves and branches); while the internodes, by elongation, stretch the nodes apart. The internodes thus give a stem or a branch its length, while the nodes produce its lateral members. A node, therefore, is a group of vegetative cells with remarkable powers of reproduction, capable of producing a new stem (branch) with its leaves. But this is not all. If a node is covered with soil, or is even placed in contact with the soil, it can also put out roots, and thus all the parts of a new individual may appear. If such a node, with its leaf-bearing branch and roots, be cut away from the rest of the plant a complete new individual is the result. It is this reproductive power of the nodes of stems that makes it possible to use cuttings, slips, tubers (Fig. 30), etc., in producing new plants. But this reproductive power of a node may be shown by other groups of active vegetative cells as well. For example, the leaf of a begonia may be cut into pieces and each piece placed in proper soil conditions may produce a new plant. The general conclusion, therefore, is that while certain vegetative cells more commonly show reproductive powers than others, any active vegetative cell may reproduce.

When the body of an individual becomes composed of many cells, ordinary cell division results in growth of the body, without producing a new individual. In other words, the machinery of reproduction is at work, but a new individual is not produced. In the many-celled individuals the dividing protoplasts are held in a continuous framework of cell walls, so that divisions cannot result in a new individual. There must be separation from the parent plant as a preliminary to divisions that can result in a new individual. Among the lower plants this necessity is met by the protoplast becoming detached from its inclosing wall and escaping from the parent plant. This freed protoplast is a *spore* (Fig. 31). It does not differ from other protoplasts in power, but in opportunity, for, separated from the parent plant, its divisions can result in a new indi-

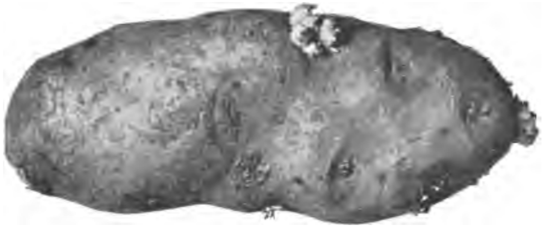


FIG. 30.—Potato tuber, showing the development of "sprouts" that will produce new plants.

vidual. The freed protoplast usually divides before it escapes, thus producing several spores, but not always. It makes no difference whether the protoplast escapes before dividing, or divides before escaping; each freed protoplast can produce a new individual. A spore, therefore, is a protoplast escaped from one individual and capable of producing another one. The abundant terminology of spores, which emphasizes the secondary characters in which they differ, has obscured the essential feature which belongs to all of them. Spores are not cells "specially set apart" to reproduce, as they are often defined, but simply cells that have a chance to reproduce.

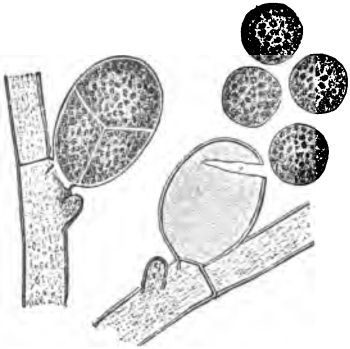


FIG. 31.—Portion of a red alga, showing a spore-case with its four spores, and another from which the spores have escaped.

A most important question is, what conditions determine the separation of the protoplast from its wall, so that it becomes free to escape. A clew to the answer is obtained from the behavior of cells in conditions unfavorable for vegetative activity. This separation of the protoplast from its wall and "rounding up" into a more compact form are very common responses to unfavorable conditions. It follows that spore-formation is a response to conditions unfavorable for maximum vegetative activity, and this has been proved by experiments. A plant kept in conditions of maximum vegetative activity grows luxuriantly, but does not produce spores; but if the vegetative conditions decline somewhat spores are produced. Whatever diminishes vegetative activity, therefore, favors spore-formation, and in nature this condition is supplied by the waning activity of the plant. It follows that spore-formation is a response to relatively unfavorable conditions for vegetative activity, by plants whose activity extends through a period long enough to encounter varying conditions. For this reason, not only many-celled plants, but also every one-celled plant that is long-lived enough, produces spores.

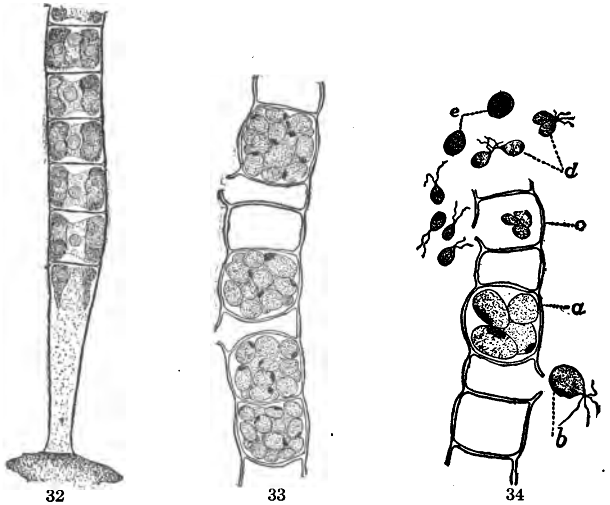
The essential condition for reproduction, therefore, is detachment from the parent body. Not only can the one-celled spore produce a new individual, but also a group of cells detached from the parent plant can do the same thing.

The power of reproducing lost parts, shown by plants and animals, has received the general name of *regeneration*. In its simplest expression it is shown in the healing of wounds. It becomes more striking when a starfish regenerates a lost arm, or when a worm cut in two pieces makes a new head end for one piece, and a new tail end for the other. If a root be cut off close to the tip the exposed cells of the stem will form a new tip;

but if the tip be cut off further back, the exposed cells will not mend the mutilated root, but active cells further back will produce a new root. This introduces another phase of regeneration, the result not being a mending or restoration of the mutilated organ, but its replacement by a new organ. In general, therefore, regeneration means a restoration or replacement of missing parts. A spore differs from a group of cells, therefore, only in the fact that all parts of the body are lost, and all have to be reproduced. It can be concluded either that regeneration is partial reproduction or that reproduction is complete regeneration. In any event, the fundamental condition of reproduction is detachment from the parent, whether it is the detachment of a single cell (spore) or a group of cells (as a node).

This second method of reproduction, by which single detached protoplasts produce new individuals, is called *reproduction by spores,* but it is merely cell division taking place in conditions that make a new individual possible. The spore method did not replace vegetative multiplication, but was added to it, as has been shown by illustrations given above, so that plants used both methods. In fact, by these two methods, which are essentially the same method, most plants are produced.

The third method of reproduction, and the last to appear among plants, is sexual reproduction. The form and occasion of its first appearance are obvious among plants, so that it is commonly said that the origin of sex can be observed. This is true in the sense that the origin of the sex cells (gametes) can be observed, but the origin of the physiological condition called sexuality has not been observed. This distinction is important, for it involves the real nature of sex. If all plants were sexual the origin of sex would be as obscure as the origin of life, but fortunately we are able to see the origin, even if we cannot understand it.



FIGS. 32-34.—*Ulothrix:* Fig. 32, portion of the vegetative filament; Fig. 33, four cells containing numerous spores; Fig. 34, fragment of a filament, showing one cell (*a*) containing four spores, another spore (*b*) escaped, another cell (*c*) from which most of the gametes have escaped, gametes pairing (*d*), and the resulting zygotes (*e*).—After CALDWELL.

The sexual cells (gametes) did not appear once for all, but appeared independently in several groups as a natural response to certain conditions. One of the green algæ (*Ulothrix*) is commonly used to illustrate the origin of gametes, but the same facts have been observed in several kinds of algæ. *Ulothrix* is a filament of cells which is entirely vegetative during the early part of its life (Fig. 32). So long as the conditions for vegetative activity are at their maximum, the filament remains vegetative. When vegetative activity begins to wane, spores are formed and discharged (Fig. 33). These spores are ciliated cells, able to swim actively in the water medium into which they have been discharged. Any protoplast in a filament may produce spores, and the variability in the number of spores formed by a single protoplast is noteworthy. The whole protoplast may escape as a single spore, but it may divide and produce two spores, or the division may go farther, and four to sixteen spores may be discharged. As the spores discharged by a single protoplast increase in number, naturally they decrease in size. As conditions for vegetative activity continue to wane, the spores become more numerous and smaller, until finally, as the plant approaches the end of its vegetative activity, the spores become so small that they do not germinate (Fig. 34).

Occasionally one of these very small spores has been made to germinate, but the result is a very dwarf individual. However, these smallest spores are observed to pair and fuse, producing a fusion cell which is able to germinate (Figs. 34 and 35). This pairing and fusing is the sex act, and, therefore, these smallest spores have become *gametes,* and the fusion cell is a fertilized egg (*zygote*). Gametes, therefore, are derived from swimming spores, but the difference is much more fundamental than one of size. At first it was perhaps natural to suppose that the smallest spores could not germinate simply because they do not contain a sufficient bulk of nutritive material, and that by pairing and fusing the bulk is increased enough to permit germination. That such an interpretation of the facts is very crude and misleading will become evident a little later.

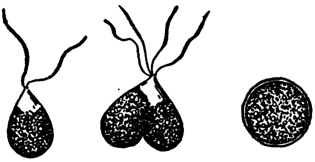


FIG. 35.—Sex act of water net (*Hydrodictyon*) : *A,* gamete; *B,* gametes fusing; *C,* zygote. —After KLEBS. From Coulter, Barnes and Cowles' "Textbook of Botany."

It will be noticed that in general there is a difference in time in the origin of spores and gametes. When conditions for vegetative activity are at a maximum neither spores nor gametes are produced; when conditions become less favorable spores begin to appear; and when the plant approaches the end of its vegetative activity gametes appear. It follows that spores and gametes are responses to different conditions. These conditions have been controlled experimentally among algæ. In the natural environment these three functions of the plant are associated with the changing season. The season begins with vegetative activity; later, the conditions favoring luxuriant growth decline and spores appear (at this stage the multiplication of individuals is the greatest); finally, gametes appear in connection with the conditions that are bringing the activity of the plant to a close.

The general conclusion, therefore, is that gametes appear as a result of the aging of cells, and that they are produced by plants whose activity extends through a period long enough to encounter a variety of conditions.

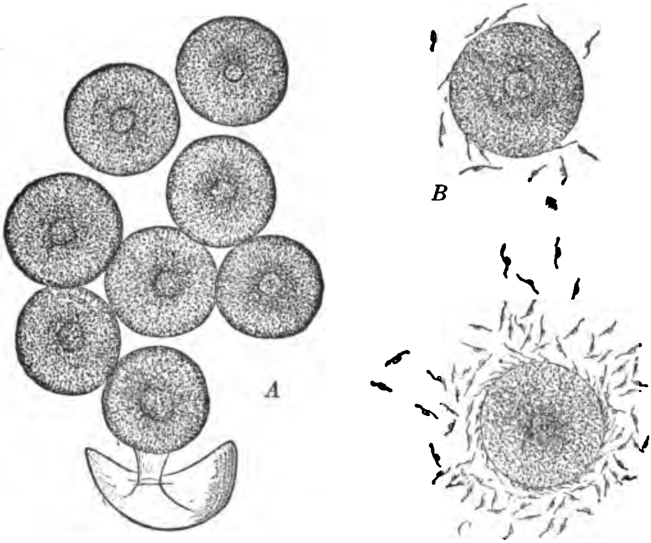
But what induces gametes to pair and fuse? This is the fundamental question. The spores from which gametes are derived do not behave in this way, and, therefore, in passing from spores to gametes some change in the physical constitution or chemical composition of the protoplast has occurred, and this change is the real origin of sex. The pairing of gametes, which means a mutual attraction, indicates that the two pairing gametes are unlike in some way, the unlikeness being comparable to the unlikeness of two poles of a battery. Since the first gametes are all alike in size and behavior, the plants producing them were called "unisexual." It is obvious that if there is a sex act at all, there must be two sexes, for although two gametes look and behave alike, if they pair and fuse they must be different. The difference of spores and gametes in size, therefore, is not the essential difference, although it seems to have been the occasion of developing the essential difference. That relative size is not essential is also indicated by the fact that later in the history of plants one of the pairing gametes (the egg) becomes much larger than a spore, and still it functions as a gamete, and not as a spore.

When one knows that the essential fusion, so far as heredity is concerned, is a fusion of the male and female nuclei, and realizes the great complexity of a nucleus, the sexual fusion must be a very intricate performance. It means that two cells contribute two complex mechanisms, which must be organized together into a single mechanism. The problem might be likened to a head end collision of two engines, which results in a single, more powerful engine.

It is interesting to note the apparent significance of sex when it first appears, that is, the rôle it plays in the life history of a plant. The fertilized egg (zygote) does not germinate immediately, but develops a thick wall and passes into a dormant stage (Fig. 35). It has become customary to speak of such a zygote as a resting cell. In any event, in such plants as we are considering, it is the cell which carries a plant over from one season to the next. The spores have multiplied plants during the season, but the zygote appears at the end of the season, and starts again at the beginning of a new season. So far as the life history of such plants is concerned, therefore, the rôle of the sexually produced zygote is not so much reproduction, that is, to multiply individuals, as protection, the chief work of reproduction being performed by the spores. Of course this is a superficial view of sex, but it is the most obvious result of sex in low plants. The explanation of the situation seems obvious. As has been stated, the zygotes are produced under conditions unfavorable to vegetative activity, when the parent plant is coming to the end of its season. It follows that the very conditions that favor zygote formation would inhibit the germination of zygotes, and they respond to the unfavorable conditions with their thick walls and dormancy. The fact that a zygote becomes a dormant cell, therefore, is not a peculiarity of zygotes, but of the conditions under which they are formed.

As an interesting confirmation of this point of view it may be said that when zygotes germinate at the beginning of a new season they either produce a new individual directly or produce spores. The production of new individuals means conditions highly favorable to vegetative activity, while the production of spores means conditions less favorable to vegetative activity. The protoplast of a zygote, therefore, is either a vegetative protoplast, or a spore-forming protoplast, dependent upon the conditions. A zygote is more apt to produce spores than a new individual, for the sequence of conditions at the opening of a season are more likely to be just the reverse of those at the close of a season. As the season progresses from its height toward its close, there is first vegetative activity, and then spore-formation; and as a season opens there is first spore-formation, and then vegetative activity.

What is called differentiation of sex means that gametes, after their first appearance as similar cells in



FIGS. 36-38.—Gametes of rockweed (*Fucus*): Fig. 36, the eight eggs discharged from the oogonium; Figs. 37 and 38, eggs surrounded by swarms of swimming sperms.—After STRASBURGER.

the lower plants, later become visibly different in the higher plants. They are physiologically different from the first, as has been shown, but eventually they become morphologically different, so that they are recognizably male and female. One of the pairing gametes becomes relatively very large, and at the same time passive, losing all of its motility, and is called the egg, while its partner remains small and active, and is recognized as the sperm (Figs. 36-38). This great increase in the size of the female gamete is due to an increase in the bulk of the cytoplasm. Since the cytoplasm of a protoplast is associated with the nutritive capacity of the cell, it follows that the nutritive capacity of the female gamete has been much increased. On the other hand, there is no such extreme change in the bulk of the nucleus. Since the nucleus of a protoplast is associated with reproduction and heredity, it follows that the reproductive capacity of the female gamete, so far as heredity is concerned, has not been increased. It contributes no more in the way of inheritance than it did when it was no larger than the male gamete. The amount of cytoplasm, therefore, is a secondary feature in reproduction, just as are motile organs.

The rôle of the cytoplasm in sexual reproduction has been a subject of discussion ever since it was concluded that the nucleus is the organ of the cell concerned with inheritance. If the cytoplasm contributes nothing to inheritance, why does it become such a conspicuous feature of the egg? It was natural to conclude that it contributes nutrition to the process of nuclear fusion and to the subsequent development of the embryo. This is certainly a function of the cytoplasm, and a very important one; but recent investigations indicate that it is not the only function, and probably not the most important one. These investigations indicate that as the egg matures there appears in the cytoplasm a substance necessarily related to the act of fertilization. This substance is produced at a certain stage in the development of an egg, and at that stage fertilization can occur; but it is not effective long, so that, if a particular period in the history of the egg is passed, fertilization cannot occur; just as it cannot occur before this physiological moment. If this substance is present in the egg the contact of the appropriate sperm stimulates it into activity, and the machinery of fertilization is put in motion. This substance has been described by Lillie, in connection with his studies of fertilization in marine animals, and named *fertilizin,* and it is this fertilizin that is thrown into action by the sperm. This added rôle of cytoplasm makes it essential to the act of fertilization, even if it is not concerned in inheritance.

An interesting question is introduced by the fact that nuclear fusions occur in plants that do not result in reproduction. When two protoplasts fuse, therefore, and do not produce a new individual, their cytoplasms or nuclei or both must differ in some way from those of functioning eggs and sperms. The reason that such a fusion call does not produce a new individual, as does a fertilized egg, is evidently connected with the constitution of the cytoplasm, which does not permit fertilization, or with the constitution of the cell organized after the fusion, for many cells (as spores) even without fusion produce new individuals. This fact suggests the idea of a possible adjustment of one nucleus to another before fusion can result in a reproductive cell, and this mutual adjustment probably lies at the basis of sex reproduction. If two complex nuclei are to unite in the formation of a single complex nucleus, organized so that it can proceed with the divisions that result in a new individual, there must be some special mutual adjustment, as well as the necessary machinery to produce nuclear fusion.

The ideas of fertilizin and of mutual adjustment of nuclei also suggest an explanation of the fact that sperms and eggs vary in their ability to fuse. It is commonly said that a certain amount of "affinity" is necessary between sperm and egg before effective fusion can take place. The degree of affinity is extremely variable, as appears in experiments with hybrids. In some cases even sexually related species will not cross; in other cases almost all the species of a genus will cross freely; and in some cases even genera are known to cross. The necessary fertilizin and mutual adjustment of male and female nuclei limit the range of hybridization, and forbid sexual reproduction in general by unrelated forms. Even when the necessary fertilizin is present the sperm may not be able to "activate" it. This also suggests a reason why sometimes the sex act between two individuals close enough in affinity results in sterility; for some reason the two nuclei are incapable of uniting in the organization of a cell able to initiate the series of divisions that result in a new individual.

All this has to do with the mechanism of sex, which must not be confused with the significance of sex. Two mechanisms must be mutually adjusted, and, therefore, sex reproduction is more limited in plants than other kinds of reproduction, because it is more complex. We have seen that the real significance of sex is not reproduction, which is abundantly provided for in other ways, but to secure something in connection with reproduction which the other methods do not, at least to so great a degree. The most rational conclusion seems to be that the sexual fusion secures an amount and a constancy of variation that no other method of reproduction can. Two cells of different ancestry, inheriting characters from two independent lines, unite to form a new cell. This gives a combination of characters for selection that is impossible in any other method of reproduction, the result being that literally no two individuals are exactly alike. Sexual reproduction, therefore, secures extreme individuality, and it is individual variation that makes evolutionary processes possible. The cell fusion which precedes the production of a new individual is not necessary to reproduction, but it is necessary to make the individual produced differ from every other individual. The extensive and varied evolution of the plant kingdom, therefore, has arisen chiefly from the abundance of variable material furnished by sexual reproduction. There is variation apart from sexual reproduction, but it is enormously multiplied by sexual reproduction.

A striking illustration of the fact that any active protoplast may be able to reproduce under favorable conditions is shown by the phenomena of parthenogenesis and polyembryony. Parthenogenesis means that an unfertilized egg produces a new individual. In this case a well-nourished gamete, without any fusion, starts the series of divisions that result in a new individual. This is simply what any well-nourished spore or protoplast can do if given the opportunity. Polyembryony in seed plants means that two or more embryos may be formed in a seed instead of the usual solitary embryo. In this case there is only one egg, so that the extra embryos have been produced by other protoplasts. In one recorded case of an onion five embryos were found in a single seed, so that at least four protoplasts had functioned as though they were spores or fertilized eggs.

SUMMARY

There are three forms of reproduction among plants, which are related to one another historically.

Vegetative multiplication is the most primitive method, which at first was represented by the division of a one-celled individual to produce two new individuals. In other words, it is merely cell division, which is a universal power of active protoplasts (cells). This method is used throughout the whole plant kingdom, the difference in detail being that in many-celled plants groups of vegetative cells are concerned in producing new individuals more often than a single vegetative cell.

Spore reproduction was the next method introduced in connection with plants with a longer life history. In general, these are many-celled plants in which the ordinary cell division results in the growth of the individual, rather than in producing new individuals. Spores are simply protoplasts detached from the parent plant, so that cell divisions have an opportunity to result in a new individual. Spores are produced in response to unfavorable conditions for vegetative activity, and by them the largest amount of reproduction among plants, that is, the multiplication of individuals, occurs. It may be noticed that a spore differs in no essential from an ordinary protoplast, except that its detachment from the parent plant gives it the opportunity to produce a new plant.

Sexual reproduction was the last form of reproduction to appear, and the sexual cells (gametes) are derived from spores in response to still more unfavorable conditions for vegetative activity near the close of the growing season. The essential difference between spores and gametes, however, is physiological, the gametes pairing and fusing so as to produce a new cell (the fertilized egg) capable of giving rise to a new individual. Pairing and fusing imply that the two gametes are physiologically different and mutually attractive. At first the two pairing gametes are alike in appearance and behavior, but with the evolution of sex they become very much unlike in appearance and behavior, so that the large passive egg and the small active sperm are recognizably female and male. The significance of sexual reproduction is not primarily the multiplication of individuals, for among plants this is accomplished chiefly by other methods; but apparently it results in securing in connection with reproduction the greatest amount of individual variation among the progeny, thus greatly accelerating the evolution of plants.

The practical application of this to the plant-breeder is that new forms are multiplied by sexual reproduction rather than by vegetative multiplication; that sexual reproduction is to be used to secure variation and vegetative multiplication to secure constancy; and that many things may be done with vegetatively propagated plants (such as graftings, cuttings, and layerings in fruit propagation, and the use of tubers, bulbs, etc.) which cannot be done with those necessarily propagated by seed, which involves the sex act.

CHAPTER VI

MASS CULTURE

Mass culture, or mass selection, is often spoken of as the old method of plant-breeding, the inference being that it is now a method abandoned by those who have advanced in scientific plant-breeding. In the history of plant-breeding mass culture is an old method, but it is far from being abandoned. It has its limitations, but it is still indispensable. It has been developed to its greatest efficiency in Germany, and therefore it is often called the "German method." When one realizes what has been accomplished by mass culture in changing cultivated plants during the last century, making them immensely more productive and desirable, he should not infer hastily that a new method can replace it entirely. The new methods have simply been added to the old one, and all of them are in vogue, each having its limitations and all necessary to secure the best results.

The original selection of wild plants for cultivation seems to have been from the wild grasses whose grains were used for food, thus starting the cultivation of cereals. This was the beginning of mass selection, and it is yet more practiced in the improvement of cereals than of any other crops. The original selection was probably no selection at all so far as distinguishing the more desirable individuals was concerned. As crop succeeded crop there may have been an unconscious selection for seed; in any event, the plants changed slowly in the direction of man's needs. Finally, unconscious selection merged into intelligent selection, and improvement became rapid. The mass culture to be discussed is, of course, that which is under the guidance of an intelligent selection. It must not be supposed that the bringing of wild plants into cultivation improved them in every particular. For example, since the discovery of the wild original of wheat, to be described in a later chapter, it is known that, although wheat has probably improved in desirable qualities of grain through the many centuries of its cultivation, the plant as a whole has deteriorated. The hardy wild races have been so pampered by cultivation as to become much less resistant to drought and disease. Wild races are always better equipped plants for the conditions of nature; but cultivated races have developed qualities more useful to man.

By mass culture is meant that continuous selection for certain characters, generation after generation, which Darwin called artificial selection. It is a slow increase of small variations in a direction guided by man. The name "mass culture" or "mass selection" has been given to it because in this process many individuals are selected, rather than one individual. The selection of one individual to breed from is called "pedigree culture." There is no question concerning the fact that cultivated plants can be changed in directions desired by man by mass selection, for the history of plant-breeding is full of such evidence, but it is a question whether mass selection can secure new forms. A sharp distinction must be made between *improved* forms, which are inconstant, and *new* forms, which are constant; for the history of plant-breeding shows that mass selection produces improved forms, but it cannot show that it has ever produced new forms. Of course, by improved forms we mean merely changed forms that are better suited to man's purposes.

How mass selection is carried on may be described in a general way. Suppose a plant-breeder wishes to secure a strain of wheat with larger heads than those possessed by the strains in ordinary use. From his field of wheat he selects the largest heads, perhaps hundreds of them, and from these heads he secures the seeds for planting. From these selected seeds he secures a second crop, and again selects the largest heads for seed; and this performance is continued year after year, until the character of larger heads has become an established feature of the strain. In this continuous selection the character of larger heads is chosen, the average size of the heads increases from generation to generation, and the final result is the summation (''piling up'') of small variations. When it is said that by continuous mass selection the character of larger heads becomes ''established'' it is not meant that the desired character is absolutely permanent or fixed. Mass selection deals with fluctuating variations, and these are by definition inconstant. A character becomes established by mass selection, therefore, when it appears in a majority of the individuals, but it is not expected to appear in all the individuals. In fact, it only continues to be established by using continuous selection. The process necessary to attain a character must be continued if it is to be maintained.

When this supposed strain of wheat with larger heads comes into the hands of the ordinary farmer very probably he does not continue the selection for large heads, but uses as seed for a second crop the product of the first one without special reference to the size of the heads. This means that the average size of heads will be lower in the second crop than in the first; and in the third crop lower than in the second; and so on until the ''improvement'' has practically disappeared. In other words, the farmer observes that his desirable strain of wheat is ''running out,'' and his remedy is to send to the plant-breeder for ''guarded stock'' for planting. Guarded stock means simply crops that have been kept from ''running back'' by continuous selection.

This is a very simple illustration of mass selection, but it may be applied in principle to any mass selection. The greatest variety of characters are chosen for selection, not only characters that involve structure, as the size of a head of wheat, but more often characters that involve chemical composition, as some special quality of a grain of wheat. For example, a grain of corn contains a region of starch storage ("starchy endosperm") and a region of protein storage ("horny endosperm"), and it is very common to select maize so as to increase one or the other of these regions, dependent upon the use to which the grain is to be put.

Most frequently some combination of characters is sought rather than a single character. For example, in selecting maize for size or quality of ears the habit is to select also for vigor of body. In other words, a vigorous plant is the first character selected, and then one or more other characters are combined with it. Usually certain characters belong together, so that in selecting for one of them the others are carried along with it. The selection of maize has been taught more generally than that of any other crop, both because it is the most important American crop, and because selection is comparatively easy. As a consequence, continuous selection of maize by the farmer ought to become relatively efficient. To arouse interest and to develop facility in selection, as well as to stimulate interest in agriculture in general, there has been an extensive organization of "corn clubs" for boys in rural communities. The United States Department of Agriculture is so much interested in these clubs that it issues bulletins for them and their contests, and has a specialist in charge of the club work. The two chief factors in the selection of maize are a suitable plant and a suitable ear. The plant should be vigorous, with all its members well developed; the selected ear should be early maturing, large, sound, well shaped, with straight and compact rows of grains, and the cob about half the diameter of the ear (Fig. 39).

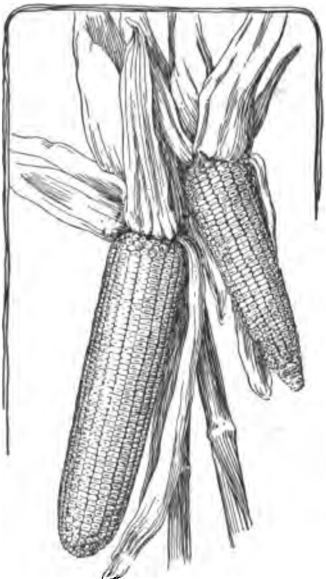


FIG. 39.—Two ears of maize, showing a desirable ear for selection (at the left) and an undesirable ear (at the right); the former has been derived by selection from the latter.

Associated with seed selection is seed testing, and this has become a very important enterprise. All sorts of corn-testers have been devised with all degrees of exactness. In general, the germinating power is greatest the next season after the seed is produced, which, of course, is the usual period in nature between seed production and seed germination. This implies that in general the germinating power of a seed diminishes as it becomes older, until finally it cannot be made to germinate at all. Failure to germinate at all plainly indicates poor seed, but unusually slow germination or feeble seedlings indicate declining power and relatively poor seed. Seeds may "sprout," that is, the inclosed plantlet may break the seed coat and begin to emerge, but sprouting is not a complete test, for there may not be power enough to carry the germination to its completion. The direction for club work is that no lot of grains should be used for planting that do not show by the testing of samples that at least 95 per cent. of them germinate promptly and vigorously. These statements concerning seed selection and seed testing of maize indicate the attention that is being given to instruct farmers so that the full results of professional mass selection may be continued when the seed is being used to produce crops.

It becomes evident that effective mass selection demands care and insight and training, and that when these are applied it results in "improvements" in almost any desired direction. It is evident, also, that, even if it cannot produce new forms, it plays a very important rôle in improving forms that are produced.

The limitations and disadvantages of mass selection are obvious, so that it must be supplemented by other methods when this is possible. The most obvious limitation is that it improves the average of many individuals rather than selects the best individual. In other words, its best result is an *average* of the better and best individuals rather than the very best individual. There are always better individuals than the average, but these are merged into the general result. Mass selection, therefore, stops short of the possibilities actually in sight. Probably the chief reason it continues to be used instead of individual selection (''pedigree culture'') is that it is a wholesale method, resulting in great numbers of improved individuals in a comparatively short time. As a commercial proposition, therefore, the market can be supplied by improved strains developed by mass selection at a rate that individual selection could not approach. What is needed, in practice, is a whole population that averages well, rather than a few individuals that are better.

A disadvantage of mass culture is the time involved, which extends through several years before the strain becomes established enough to be ready for the market. It is a question whether this loss of time in mass culture would not permit pedigree culture to overtake it in the number of desirable individuals. The time involved of course varies widely with the plant under culture and the characters being developed. It has been stated that commercial plant-breeders, who deal with a great variety of plants, estimate an average of six years for the production of a desirable improved strain by mass selection. This means that a longer time is required for some plants and a shorter time for others. I have no means of knowing whether this estimate is fair or not, but it serves to illustrate the fact that a considerable amount of time is involved, which means a large expenditure of professional training.

An historical case of mass culture, described by DeVries, is that conducted by Rimpau of Germany in the production of a well-known race of rye which is now cultivated throughout central Germany. He selected all the ears from his rye fields that seemed noticeably better than the others, and thus mixed all the seeds from numerous individuals, for planting. This selection was continued through twenty years, until a very superior race was obtained. Finally, the seeds were sown for multiplication without further selection. It took three or four years of multiplication to secure seed enough to sow the whole farm; but after that the new rye became very profitable. Of course it became profitable, both to the farmer and to the seed dealer; profitable to the farmer because he could raise crops of rye of larger yield and better quality; but chiefly profitable to the seed dealer because the farmer was compelled to return to him frequently for "guarded stock."

Associated with the time involved is the labor. To make mass selections that are consistent through a succession of years is not merely very laborious, but it is also very critical. A mere laborer cannot be depended upon, for the selection demands a keen eye for the combination of characters that the selected individuals must show. In other words, it is professional work. For this reason farmers cannot be depended upon in general to continue the selection. In such a plant as maize it has been found practicable to give general instruction in selection, as has been indicated above, but even in the case of maize, if farmers were competent to make a continuous selection the size of the population with which they deal in their extensive fields, compared with the small experimental plots of the seed dealers, makes guarding against the crossing of desirable with undesirable individuals impracticable.

Perhaps the greatest disadvantage of mass culture is this inconstancy of the result in the hands of the crop-producer. In the hands of the trained plant-breeder the result is constant enough, but in the hands of the crop-producer it is not, for, as has been said, he cannot continue the discriminating selection. Of course this fact is one of the assets of the commercial plant-breeder, for the crop-producer must apply to him repeatedly for fresh seed that has been kept up to standard by continual selection. The amount of time and labor given in mass culture to secure an inconstant product would have forbidden the method long ago but for the fact that an inconstant improvement is far better than no improvement, and perhaps the additional fact that the inconstancy of this particular kind of product is commercially valuable.

In spite of the disadvantages of mass selection, it remains as one important method in the improvement of cultivated plants, and it is also often very useful as one factor in a combination of processes. And still it must be recognized that with mass selection alone there is probably no production of new forms and also a definite limit to improvement. In other words, the old characters may be changed more or less, but no new character is introduced. In the nature of things a new character is constant in the sense that if it appears at all it will reappear in some form in all the progeny, while a changing old character continues to be a variable feature in the progeny. The statement that mass selection is a means of averaging results rather than of selecting the best may be illustrated by the methods used in animal-breeding. An animal-breeder does not expect to get his best results by improving a whole pasture full of horses *en masse.* He selects the most desirable individuals and pedigrees them, securing, not an average improvement, but the best improvement. In the same way mass selection among plants cannot hope to reach the best results.

An additional danger in the cultivation of such extensively massed crops as the cereals must be reckoned with. Any field of oats or wheat, and notably maize, consists of an extensive and very mixed population. These individuals may average well, but there are many below the average as well as above. In forming seeds these individuals may cross freely, since the pollen is blown about by the wind, so that an inferior and a superior individual are just as apt to cross as two superior individuals. This means that the seeds thus produced will probably lower the average of the next generation, so that the average subsides from generation to generation, or at least is kept from advancing, even with some attention to selection. This danger increases as the population becomes larger, and it diminishes as the population is smaller and can be brought under more rigid control. This means that even when a very desirable race is obtained that seems constant, and in no danger of losing its distinctive characters, there is bound to be more or less lowering of the average of excellence. This can be offset only by a constant and rigid application of the principles of selection.

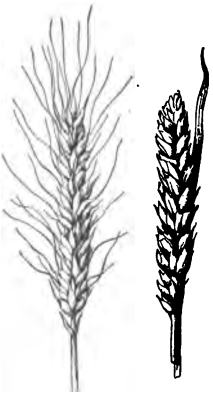


FIG. 40. — Bearded and beardless wheat. — After Internat. Encycl.

Attention should be called to the fact that all cereals are not alike in the freedom of pollination. For example, the ordinary cultivated races of wheat are self-pollinating (Fig. 40), so that a race of wheat is more apt to retain its characters than an open-pollinated plant. On the other hand, the pollination of maize is necessarily open, since the stamens and pistils are in separate flowers, those containing stamens forming the

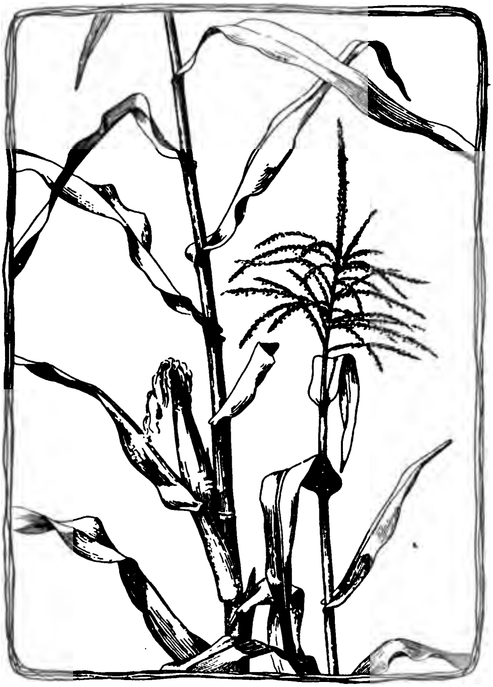


Fig. 41.—Maize: the plant at the right shows the staminate flowers forming the terminal "tassel"; the plant at the left shows the "ear" (a close cluster of pistillate flowers) in the axil of a leaf and inclosed by the "husk," at the end of which the long styles ("silk") are exposed.—After DeVries.

"tassel," while those containing pistils form the "ear" (Fig. 41). As a consequence, a race of corn is the most difficult cereal to keep up to standard.

It is evident that this danger disappears in the case of crops propagated vegetatively rather than by seeds. For example, when the potato, through selection, has been brought up to a good average of desired characters its propagation by tubers insures against the danger of unfavorable crossing. For this reason all plants propagated by bulbs, tubers, cuttings, etc., "hold their own" through successive generations much more rigidly than do those propagated by seeds.

SUMMARY

Mass selection, which means the selection of a desirable group of individuals, when continued from generation to generation, results in a slow building up of the characters desired, in some cases involving very great changes from the original forms. Furthermore, the improvement obtained by mass selection is the average improvement of an extensive population rather than the extreme of improvement shown by certain individuals. To maintain even this average improvement rigid selection must be maintained, or the average will be lowered with every generation. This is more imperative in the case of crops propagated by seeds, as cereals, than in the case of those propagated vegetatively; for in addition to the inferior individuals that selection avoids, superior individuals may cross with inferior ones and thus add to the inferior population. In spite of its limitations and disadvantages, mass selection is probably the most available method for improving crops that are grown on a large scale, and for securing a large number of desirable individuals rapidly; and also it must continue to be the best method of raising and maintaining the general average of a crop.

CHAPTER VII

PEDIGREE CULTURE

It was natural that mass selection should continue to be the prevailing method of plant-breeding so long as natural selection was the dominant biological interest, for it is based upon the principles of natural selection; in fact, it is applied natural selection, the necessities of men being substituted for the necessities of nature. But when theories of evolution inevitably led to experimental work in heredity a method more definite and precise than mass selection became necessary. This method of greater precision was *pedigree culture.* It is surprising that the pedigree culture, so common in connection with the breeding of fine stock, had not suggested much earlier the use of the same method in plant-breeding. It was introduced in the breeding of plants when it was discovered that absolute control over individuals was necessary in securing definite knowledge in reference to inheritance of characters. The first record we have of strict pedigree culture among plants is in connection with the experimental work of Mendel, the results of which were published in 1865, but did not become current until more than thirty years later. The work of Mendel will be described in the next chapter. Since that time pedigree culture has developed extensively as a method of plant-breeding, and is now being used in connection with all work upon heredity.

Pedigree culture as a method is another illustration of the important practical results that may come from a purely scientific investigation. Established as a means of studying the laws of heredity, it is now being applied as a means of securing desirable plants in a most effective way. By means of this method it has been possible to secure desirable plants in numbers and in kinds that were once thought to be impossible, for the investigation of characters has shown the method of securing characters. It is for this reason that in a book dealing with practical plant-breeding it is necessary to know something of the methods of scientific pedigree culture.

Pedigree culture of plants means complete control and record of every individual in a series of cultures, running often through several generations. The control has to do with pollination. If the plants are self-pollinating, care has to be taken that no foreign pollen reaches the pedigreed individuals. In most studies of heredity, hybrids are used, which means the use of foreign pollen, and in such cases artificial pollination must be resorted to. To pollinate artificially a large group of individuals, and to isolate them absolutely from all other pollen than the kind desired, demands an amount of training and technique that may not be appreciated. It is also necessary, in experimental work on heredity, to secure plants that are easily handled and that have short generations, for the value of the results depends upon the number of generations observed.

The first practical application of pedigree culture was made at the Swedish Experiment Station at Svalöf, under the directorship of Nilsson, and will be described in a later chapter. It was used to secure results that mass selection had failed to secure. As has been stated, mass selection can only obtain a good average result, and the average is inconstant unless careful selection is continued. Pedigree culture in its practical application involves the selection of the most desirable individual, a better individual, of course, than any average, and the progeny obtained from this individual is relatively constant. This constancy of a pedigreed series in the features in which they differ from their relatives was demonstrated by DeVries in the experimental work that formed the basis of his theory of mutation. As a consequence, the scientific work of DeVries underlaid the practical work of Nilsson, and, conversely, the practical work of Nilsson furnished arguments in favor of mutation.

The use of scientific pedigree culture has been developed by two groups of investigators, groups that do not differ in purpose, but chiefly in method. A brief account of these two groups will help to an understanding of the practical applications of pedigree culture to be given later.

BIOMETRY

One of these groups of investigators, called biometricians, uses the statistical method of recording data. Instead of dealing with the variation of a single individual, they deal with the average variation of a population, that is, many individuals representing a given species. It is really a method of observing how a population as a whole behaves through a series of generations; that is, whether the average is remaining constant, or whether it is shifting, or whether it is splitting up into distinct groups. No observation of a single individual could secure such data. The name of this group of investigators is explained by the fact that the method of securing data is by measurements and countings of a series of individuals and then striking the average. For example, characters that involve either size or weight are measured, while of course those involving number are counted. As an illustration, almost any species of aster may be used, in which the varying characters involve the number of rays and also the length of rays.

The necessity for pedigree culture in such work appears when it is known that the average means nothing unless the individuals measured or counted represent what is called homogeneous material, that is, a common stock, and not a miscellaneous assortment of individuals assumed to represent the same stock. It is evident that even the purest seed that can be obtained from seed dealers has been secured from mass cultures, and necessarily represents a complex mixture of individuals. In fact, a field of wheat or of maize raised from the purest market seed is a bewildering mixture of different kinds of individuals. No facts of heredity can be obtained from such a mixture. The only way it is possible to be sure that a thousand individuals represent a homogeneous assemblage is to pedigree these individuals from some common stock. Therefore, biometricians have helped to develop the technique of pedigree culture to its present perfection of control. The first man to suggest the statistical method of recording biological data was the English economist Malthus (1766-1834), whose famous ''Essays on Population'' has made his name very familiar as the author of the so-called ''Malthusian doctrine.'' This seems to have been the first application of statistics to biological phenomena, but it had nothing to do with the study of heredity. It was a statistical study of the ratio of increase of the human population, with the conclusion that the population always tends to increase faster than the production of subsistence, and therefore that there is absolutely no cure for poverty.

It was this piece of work that suggested to Quetelet (1796-1874), the Belgian mathematician and astronomer, the application of statistics to a study of variations, which, of course, is one of the important problems of heredity. Quetelet is often called an anthropologist because he applied his statistical method of measurements to different parts of the human body. He discovered that the variations in these measurements follow definite laws, and he formulated a law which has since been called by his name. This law is cited by biometricians as the starting point of their work.

The real development of biometry as an elaborate method is due, however, to a group of English investigators. In 1899 Francis Galton published his "Natural Inheritance," which was the pioneer book on biometry, and established it as a definite subject. Galton was a grandson of Erasmus Darwin, and Charles Darwin's cousin. Extensive use of the statistical method in investigations has been made by Weldon, but the method of using statistics has been developed chiefly by the mathematician Pearson. The method of biometry has not as yet been applied in practical plant-breeding, but there is no reason why it should not be. The technique of pedigree culture, however, has been the contribution of biometricians to practical plant-breeding.

GENETICS

The name genetics has been applied to the use of pedigree culture in the very extensive study of individuals generation after generation. The sharp contrast between biometry and genetics, therefore, is that the former deals with populations and the latter with individuals. Biometry is more or less committed to natural selection, and was an early outgrowth from that theory, while genetics is more committed to mutation, and certainly to Mendelism. At present genetics is being developed much more extensively than any other method of studying evolution and heredity, so that many investigators who started as biometricians have become geneticists. This does not mean that biometry has been abandoned as a method, but that the most pressing problems are to be solved by the method of genetics.

The real founder of the "school of genetics," as it is sometimes called, was the Austrian monk, Gregor Mendel (1822-1884). The law which he announced as a result of his experiments has become the working basis of practically all investigations in genetics. In the next chapter this will be presented in some detail, but at this point an outline sketch of the work of genetics must include some facts in reference to Mendel. He conducted his experiments in the cloister garden of the monastery of Brünn, to which he belonged. He selected the common garden pea for his cultures, and after eight years of work published his results in 1865. These results came at a time when the theory of natural selection was attracting universal attention, and was directing the thought and work of biologists in general.

For this reason, perhaps, the publication of Mendel was lost sight of and remained unnoticed until 1900, thirty-five years after its appearance. It was in that year that three students of genetics discovered it simultaneously. The three investigators who really introduced Mendel to biologists, sixteen years after his death, were DeVries of Holland, Correns of Germany, and Tschermak of Austria. Since that time "Mendel's law" has formed the basis of all work in genetics.

After Mendel, the most important contribution to genetics has doubtless been the work of DeVries in developing his theory of mutation, for it stimulated the experimental study of evolution and heredity by means of pedigree cultures as no other single work has done. Working simultaneously with DeVries in Amsterdam was Correns of Leipzig, who has recently become the director of an extensive station for experimental study of evolution at Berlin. Tschermak, working at Vienna, was another one of the original trio to stimulate the study of genetics.

Since that time groups of investigators in genetics have been developed in almost every country. In England the most notable work has been done by Bateson and his associates. In the United States the Carnegie Institution has established a station for the study of experimental evolution, at Cold Spring Harbor, Long Island, under the directorship of Davenport. At the Bussey Institute, of Harvard University, Castle and

East have done most valuable work in genetics, the former with animals, the latter with plants. At the University of Chicago a very extensive series of pedigree cultures of the Colorado beetle have been carried through by Tower, for a number of years; the cultures being conducted not merely at the University, but also at the Desert Laboratory at Tuscon, Arizona, and at various stations in Mexico and in the American tropics.

A tendency of the later work in genetics is to pass beyond the mere record of observations connected with a long series of pedigree cultures, and to attempt to induce variations. Methods have been devised for influencing eggs and sperms in various ways, and the result has been the production of numerous forms differing from those produced ordinarily. In other words, experimental work is now attempting not merely to observe variations, but to produce them. The practical applications of this extension of experimental work are obvious. Not only can natural variations be detected and selected for culture, but artificial variations can be produced. In plant-breeding this extends enormously the possibilities in securing almost any kind of plant that is needed.

It is obvious that the technique of pedigree culture opens up numerous possibilities to the practical plant-breeder. Since no two individuals are exactly alike, even when produced by the same parent, there are endless variations to select from. Instead of merging these variations in some average result, as mass selection does, pedigree culture can keep them separate, and thus perpetuate numerous races. When it is remembered that great variations in cultural conditions must be met by corresponding variations in races of plants, it is evident that many results in breeding each kind of crop, rather than an average result, must be secured in order that each region may produce a maximum yield. Furthermore, with a pedigreed race of individuals the deterioration that comes from the crossing of desirable and undesirable individuals is reduced to a minimum, for all of the pedigreed individuals are better than the average of mixed races.

SUMMARY

Pedigree culture means the selection of an individual, controlling its reproduction, and keeping an exact record of its progeny. The control in the case of plants involves rigid control of pollination, so that both parents of any individual in a series of cultures may be known.

The technique of pedigree culture was developed first in biometrical investigations. Biometry is a statistical study of variations by which it can be discovered whether a given population is remaining constant or is changing its character. It does not suggest any explanation of evolution or of heredity, but records the general movements of variations, much as the weather service records the movements of atmospheric pressure. The necessity for pedigree culture in such work is that the population studied must be homogeneous, that is, made up of individuals from a common stock.

Genetics uses pedigree culture in the study of individuals rather than populations, to discover the laws of inheritance. At present genetics is the prevailing method used by students of evolution and heredity; in fact, it is the only method by which the definite facts of heredity can be secured. By means of it pure strains can be separated from mixtures, the behavior of hybrids can be observed, and the constancy of species tested.

The application of pedigree culture has revolutionized practical plant-breeding, making it possible to take advantage of the extreme variability of plants and to secure races adapted to the greatest variety of cultural conditions. It will be seen later that pedigree culture also supplies a very direct means of securing resistance to drought and disease.

CHAPTER VIII

MENDEL'S LAW

Any plant-breeder who desires to work intelligently with plants must have some knowledge of Mendel's law. As has been stated, this law is the working basis of practically all the experimental work in plant-breeding. To use a law as a working basis does not imply necessarily a belief in the infallibility of the law. Some investigators are ready to explain every phenomenon of inheritance in terms of Mendel's law; while others doubt whether all of the observed phenomena can be explained in this way. In any event, it is a powerful tool and its use should be understood.

In the preceding chapter a brief statement was made in reference to the personality of Mendel and the date of his work. Mendel (1822-1884) was an Austrian monk and abbott in the monastery of Brünn, where he conducted his experiments in the cloister garden. After eight years of work he published his results in 1865, in the *Proceedings of the Natural History Society of Brünn,* under the title "Versuche über Planzenhybriden." This paper of forty pages has become a great biological classic, having been translated into the languages of all civilized countries. It remained unknown until 1900, when it was brought to light simultaneously by DeVries, Correns, and Tschermak, as stated in a previous chapter. The cause of this curious neglect was probably due chiefly to the recent appearance of Darwin's "The Origin of Species," which was attracting universal attention; and in part to the fact that a more or less speculative theory of general evolution was more in accord with the interest of most biologists of the time than experimental work with the hybrids of peas. Genetics was not known, and the problems of heredity had not been attacked experimentally. Darwin's book came at the psychological moment for fame; while Mendel's paper came at the psychological moment for neglect.

It remains now to describe briefly the nature and the meaning of Mendel's experiments. He wished to choose for his experimental work some plant with a short generation, and also one easily cultivated. Besides these features, the various races or strains of the plant should have sharply contrasted characters. He chose the common garden pea, which has thus become the classic plant in the history of genetics. It seemed to meet all of the requirements Mendel had in mind. With the aid of greenhouse cultures two or three generations can be secured in a single year, the plants are easily grown, and the contrasting characters are distinguished sharply. For example, in the various races the colors of the flowers are purple, red, or white; the mature seeds are smooth or wrinkled; the stature of the different races is either distinctly tall or just as distinctly dwarf. There would be no trouble in recognizing the presence of such characters as these.

It will be observed that all students of genetics, beginning with Mendel, use hybrids in their work. The reason for it is obvious, but perhaps should be stated. In studying the laws of inheritance it is necessary to discover the contribution of each parent to the progeny. If the parents are very much alike these contributions cannot be distinguished; but if they differ in strongly contrasted characters there can be no question as to what each parent has contributed. For example, when Mendel crossed a purple-flowered race with a white-flowered one, the progeny would show at once just what each parent had contributed in color of flowers. In other words, the use of hybrids in genetics resembles the use of the microscope in morphology; it makes facts obvious that otherwise would be invisible. At the same time it must be remembered that the laws of inheritance made obvious by the use of hybrids apply as well to inheritance from similar parents. What is true of inheritance in hybrids, therefore, is true of inheritance in general.

After the selection of his material, the high quality of Mendel as an investigator was shown by the method he adopted. Each one of the races of peas which he handled possessed a number of characters, and it would seem natural to watch the behavior of all of these characters through the successive generations, but Mendel concluded that he should focus his attention upon one character at a time, just as a microscope is focused upon one object at a time. Therefore, he traced the color character through a series of generations, and paid no attention to the other characters, and so for each character in turn. At the conclusion of his experiments he discovered that all the characters thus traced through independently were behaving alike, and he was able to formulate his general law.

One of the first things he discovered was that in crossing two plants it made no difference which was the pollen parent and which was the ovule parent; the results were the same. In experimental work of this kind it is expected that the investigator will perform what is called reciprocal crossing. For example, if Mendel had used a purple-flowered pea as the pollen parent and a white-flowered pea as the ovule parent, the reciprocal crossing would be to perform another experiment in which a purple-flowered form would be used as the ovule parent, and the white-flowered form as the pollen parent.

The easiest way to understand Mendel's results is to take a simple illustration. For our purpose the crossing of purple-flowered and white-flowered races may be used. When the purple-flowered and white-flowered forms are crossed, the progeny consists of plants which have received characters from two kinds of parents, and therefore are hybrids. In genetics this hybrid generation is spoken of as the F_1 generation. The important fact connected with this generation is that in our experiment every individual has purple flowers, although one of the parents was white-flowered. The natural question is, what has become of the character of whiteness? Has it disappeared, or has it been merely suppressed? It will be discovered that in the next generation white-flowered individuals appear again, so that it is obvious that in the hybrid (F_1) generation the character of whiteness has simply been suppressed.

To express this situation, Mendel used two terms with reference to each pair of contrasting characters. For example, the purple character, which is contrasted with the white character in this experiment, he called *dominant,* because it dominated over the other color; and the white character, which did not express itself, he called *recessive,* which means practically the same thing as the older term latent, often applied to the idea that characters are present which do not develop. This experiment shows, therefore, that purple is dominant over white in the crossing, and other experiments with the peas showed that red is dominant over white. In the same way Mendel discovered that tallness is dominant over dwarfness, so that from pairing dwarf and tall parents, the F_1 generation would all be tall. Moreover, Mendel discovered that in his experiments there was no such thing as blending of contrasted characters. For example, in crossing a tall race with a dwarf one, one might expect that the progeny would show some intermediate stature, as though an average had been struck, but this never happened in such contrasted characters. One character or the other expressed itself as though the other were not present. Such characters as do not blend in reproduction, but remain independent of one another, are now spoken of as *unit characters,* which means that they maintain their individuality through association with all sorts of other characters.

Mendel's law really appears in the F_2 generation, that is, the progeny of the hybrid or F_1 generation. Continuing the experiment selected, the F_2 generation is made up of three kinds of individuals, in a definite ratio, which appears if four individuals are selected. One of the four will be a pure purple individual, as shown by breeding true generation after generation; a second will be a pure white individual, as shown by subsequent breeding; while two of the four will be purple individuals but will contain the white character as a recessive, as shown by subsequent breeding; in other words, these two individuals are simply like all of the individuals of the F_1 or hybrid generation. The ratio is expressed in two different ways. In one way the three kinds of individuals are indicated by writing the ratio 1:2:1. The more common way is to indicate the appearance of the four individuals by writing the ratio 3:1, which means in our experiment that there are three purple individuals to one white one. Of course, this latter expression does not show that there are two kinds of purple individuals. The accompanying diagram (Fig. 42) will make these facts clear.

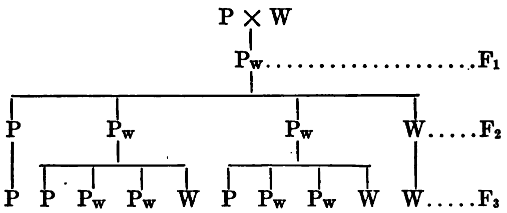


FIG. 42.—Diagram illustrating Mendel's law.

To make this result more concrete, the following illustration may be used. In planting seeds from purple-flowered peas, an occasional white-flowered form may appear. In this case it is obvious that at least one of the parents of the purple-flowered form had whiteness as a recessive character, and that there is one chance out of four that a white-flowered form will appear among the progeny. The case may be made even more concrete by applying it to one of the contrasting characters in human beings. For example, brown eyes are dominant over blue. In the case of two brown-eyed parents, therefore, if either one of them has inherited blue as a recessive character, the chances are that some of the children will be blue-eyed. If they all come true to brown eyes, the inference is that the parents have not inherited recessive blue.

In his experiments Mendel included seven contrasting characters: those of flower colors (purple, red, and white); those of stature (tall and dwarf); and those of seeds (yellow and green, and smooth and wrinkled). In every case, before crossing for contrasting characters, he determined by cultures that the characters were pure, that is, that there was no recessive associated with them. In every case the experiments resulted in an F_1 generation uniform in appearance, all the individuals exhibiting the dominant character; and in the F_2 generation there was a splitting up in the ratio of 3:1, the character that was recessive in the F_1 generation appearing again in one-fourth of the F_2 individuals. In succeeding generations, the pure individuals of the F_2 generation continued to breed true, the two characters having been completely separated in them; but the progeny of half of the F_2 generation split up again in the same ratio. In other words, in breeding from a hybrid, half of the progeny in each generation resemble the pure parents, while half continue to be hybrids.

This is a very important fact in connection with plant-breeding, for the production of hybrids is a most effective way of securing desirable combinations of characters; in fact, the results obtained by Burbank have come chiefly from successful hybridizing. Mendel's law means that, if hybrids are propagated by seeds, which of course involve the sex act, only half of the individuals in each generation will show the hybrid characters. It is evident, therefore, that the use of hybrids in practical plant-breeding, if all of the progeny are to be hybrids, must be restricted to such plants as can be vegetatively multiplied, as by bulbs, tubers, slips, etc. In general this applies to the breeding of fruits, and of course also to such tubers as the potato. This does not mean that hybridizing may not be used in connection with the breeding of cereals, which are propagated by seeds, but it does mean that in this case the hybrids will continuously split, and the result in each generation will be a partial result rather than a complete one.

To explain the behavior of contrasting characters as indicated by these experiments, Mendel formulated a theory, which has since been substantiated by studies of the structure of sexual cells. He conceived the idea that any given sexual cell (egg or sperm) could contain only one of two contrasting characters. For example, the egg of the pea could contain either the purple character or the white character, but not both; that is, two contrasting characters are mutually exclusive. Very fundamental, therefore, in connection with Mendel's law is the theory of what is called the "purity of the germ cells" in reference to characters.

There should be no confusion as to the use of the word "character" in this connection. Mendel did not imagine that it represents an actual substance being carried by the egg or sperm, but it is whatever in egg or sperm determines the development of a given character. In that sense, perhaps the word "determiner" would be better than the word character. Using it in our illustration, the statement would become that the egg or sperm of the pea could contain either a purple or a white determiner but not both. This theory explains in a very satisfactory way the results of Mendel's experimental work. For example, if an egg and a sperm, each containing a purple determiner, fuse and produce a fertilized egg, the resulting individual will be a pure purple strain. However, if the egg contains a purple determiner and the sperm a white one, or vice versa, the fertilized egg will contain both kinds, and, since purple is dominant over white, the resultant individual will be purple, but it will also contain a recessive white determiner, which may come out in a subsequent generation as a pure white strain. It will be observed that since there are two kinds of eggs in reference to contrasting characters, and two kinds of sperms, and since eggs and sperms fuse in pairs, there are only four possible combinations. These are as follows: there is just one chance out of four that two sexual cells with purple determiners will fuse, and the result is obvious; there is one chance out of four that two sexual cells with white determiners will fuse, resulting in a pure white strain; and there are two chances out of four that a sexual cell with a purple and one with a white determiner will fuse. This is exactly Mendel's law, whether its ratio be written 1:2:1 or 3:1. These statements are made graphically in the accompanying diagram (Fig. 43), the four lines indicating the four possible fusions.

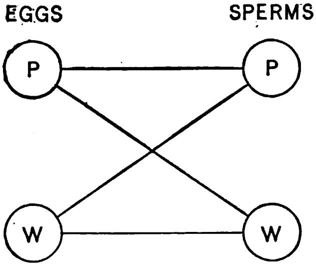
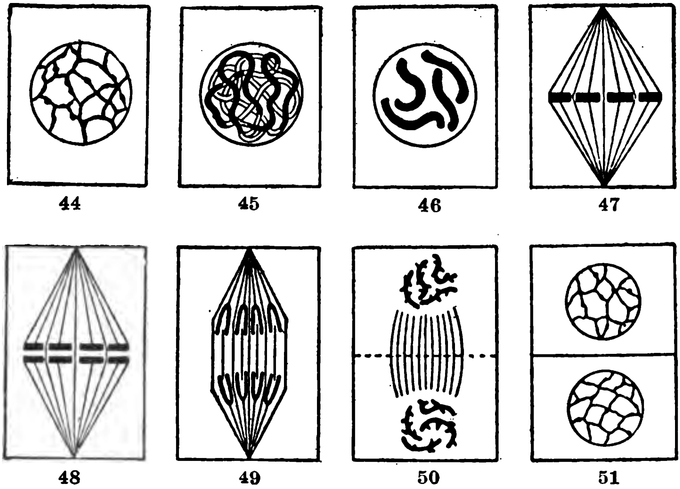


FIG. 43.—Diagram illustrating possible fusions of sexual cells.

Some account of the recent development of our knowledge in reference to what may be called the machinery of heredity will help to an understanding of the later work in plant-breeding. A living cell has the power of division, that is, it divides itself and two new cells are the result. When a plant or an animal body consists of a single cell, this division results in two new individuals and the disappearance of the old one. In the case of many-celled plants and animals, such cell division does not result in new individuals, but in what we call the growth of the body. It is obvious that when a cell divides to form two new ones, whether it results in a new individual or in growth, the laws of heredity are involved, since the process must involve the transmission from the parent cell to the two new cells of the characters which determine their resemblance to the parent cell.

In focusing attention upon this process of cell division, it becomes obvious that the organ of the cell known as the *nucleus* is responsible chiefly for cell division. Therefore, it is generally believed that the nucleus is the organ concerned with heredity. The nucleus, however, has an extremely complex structure, but there is one feature of its make-up that must be mentioned. The most compact substance it contains is distinguished from all other substances of the nucleus by the fact that it takes up stains, and is thus brought out in sharp contrast with the rest of the nucleus. This stainable substance is called *chromatin,* the name being given to



FIGS. 44-51.—Diagram of stages in nuclear division: explanation in text.—After LOCK.

it on account of this relation to stains. In an ordinary nucleus, the chromatin appears as a network through the body of the nucleus (Fig. 44). At the approach of nuclear division, which of course precedes cell division, this chromatin is observed to pass through a series of remarkable changes. In the first place, the network becomes a continuous band, looped back and forth in a tangle through the body of the nucleus (Fig. 45). Later, this band becomes separated into distinct pieces (Fig. 46). These separate pieces of chromatin are called *chromosomes,* and they represent the organized units of chromatin. If protoplasm is the "physical basis of life," as Huxley stated, it may be said with equal truth that chromatin is the physical basis of heredity. An important fact to remember is that the number of chromosomes is a fixed number in each kind of plant and animal. It is the same invariable number in every cell of the body, and these numbers vary widely when different kinds of plants and animals are contrasted. In other words, the number of chromosomes that belongs to each nucleus is one of the fixed characters of each kind of plant and animal.

While these changes in the chromatin material have been going on, there has formed about the nucleus what is known as a *spindle,* composed of delicate fibers that embrace the nucleus like the imaginary parallels of longitude embrace the earth (Fig. 47). These fibers are drawn together in two poles, resulting in an equatorial plane where they are widest apart. When the chromosomes appear, they line up in the equatorial plane with their long axes in the plane. In that position each chromosome splits lengthwise (Fig. 48), and each half-chromosome passes to the adjacent pole (Fig. 49). There they come together again (Fig. 50), end to end, the bands and network (Fig. 51) are formed, and two new nuclei, one at each pole, are the result. In the meantime, through the equatorial plane a wall has been laid down (Fig. 50), and two new cells are the result (Fig. 51). It is obvious that each nucleus contains half of each chromosome of its parent cell. Thus the succession of cell generations, just as a succession of individual generations, carries forward in unbroken line samples of each chromosome, bearing its peculiar determiners.

Having outlined the behavior of chromosomes in ordinary cell division, it is possible to understand what occurs when sexual reproduction takes place. For the sake of convenience, we may assume that an egg and a sperm, each containing two chromosomes, fuse, forming the fertilized egg. This low number is taken for convenience, and not that it is at all representative of the numbers that usually occur among plants and animals. In certain plants, notably among the ferns, the number of chromosomes in each nucleus often reaches one hundred and fifty. The number, however, makes no difference in considering the general situation. In the illustration being used, the sperm bears two paternal chromosomes and the egg two maternal chromosomes, and as a consequence the fertilized egg contains four chromosomes, two paternal and two maternal (Fig. 52). These four chromosomes remain distinct throughout the whole development of the individual from the fertilized egg, so that each cell of the body contains two paternal and two maternal chromosomes. However, this does not mean that all four chromosomes dominate; in fact, two of the four will dominate and determine the physical characteristics of the developing individual.[1] It can be seen at once that there are three possible combinations in such a domination (Fig. 52). The two paternal chromosomes may dominate, and in that case the new individual

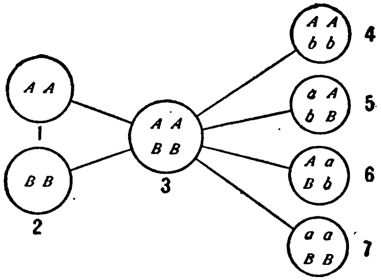


FIG. 52.—Diagram illustrating possible results of sexual fusion: *1*, sperm containing two chromosomes (*AA*); *2*, egg containing two chromosomes (*BB*); *3*, fertilized egg containing two paternal and two maternal chromosomes; *4*, domination of paternal chromosomes; *5* and *6*, domination of one paternal and one maternal chromosome; *7*, domination of maternal chromosomes.

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[1] This "domination of chromosomes" is used to illustrate a general situation, rather than to state a fact. Such a fact is not within reach of proof as yet.

will resemble the male parent. The two maternal chromosomes may dominate, and in that case the individual will resemble the female parent. There are two chances out of four that the dominating chromosomes will be paternal and maternal, and in these cases the new individual will blend the characters of the two parents. It will be observed that this is exactly the ratio of Mendel's law.

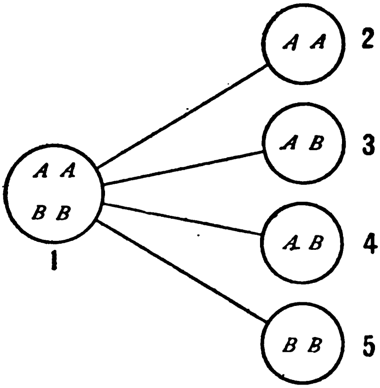

FIG. 53.—Diagram illustrating result of reduction: *1*, ordinary cell of body containing the double number of chromosomes; *2-5*, eggs or sperms containing the reduced number, and illustrating the possibilities in the distribution of paternal (*AA*) and maternal (*BB*) chromosomes.

It must not be understood, however, that this performance determines sex. The resemblance to the parent is merely in bodily appearance, so that maternal chromosomes may result in a male who resembles the mother, or paternal chromosomes may result in a female who resembles the father. When the individual with four chromosomes, two of which have dominated in its development, reaches the stage when it produces reproductive cells (eggs or sperms), the chromosomes become segregated in these cells, each containing only two. Therefore the eggs or sperms produced will be three kinds (Fig. 53): those with two paternal chromosomes, those with two maternal chromosomes; and those with one chromosome from each parent. When these three kinds of eggs pair with three kinds of sperms, it is obvious that, if a total of four chromosomes is involved, there will be at least three possible results: fertilized eggs with four paternal chromosomes; those with four maternal chromosomes; and those with a pair of chromosomes from each source. This gives the Mendelian ratio again, and shows how a recessive character, lost in a hybrid generation, reappears in the following generation, for in one-fourth of the F_2 progeny it is not associated with the character which is dominant over it. Of course, there are possible complications in these combinations that will occur to any one, but in the interest of clearness at this stage of the discussion they are omitted.

The question of sex determination has been a problem for a long time; but only in recent years has it yielded definite results. When it is said that the determination of sex is perhaps now understood, it must not be inferred that sex can be controlled. Sex determination and sex control are two very different things. In studying the sexual cells of certain animals, it was discovered that in the eggs and sperms there might be present an extra chromosome, not to be accounted for in the ordinary organization of the nucleus. This extra chromosome sometimes differs in size, sometimes in staining reaction, and always in behavior from the ordinary chromosomes. It was called the *X* chromosome, the letter of course indicating, as in algebra, an unknown quantity. These *X* chromosomes were first distinguished clearly and studied most completely in certain insects, notably the grasshopper and bedbug.

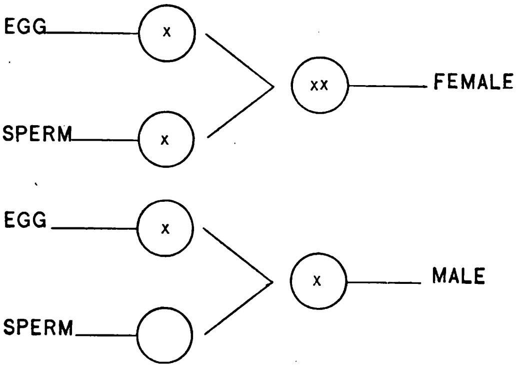

FIG. 54.—Diagram illustrating the *X* chromosome result.

As yet they have not been distinguished with such clearness among plants, but they have been detected as extra chromosomes, and often as differing in form.

These *X* chromosomes are now coming to be called sex chromosomes, because they seem to determine the sex of the individual produced by the fertilized egg. So far as known, every egg contains one of these chromosomes, and approximately half of the sperms contain each an *X* chromosome, the other half being without this body. Why it is that each egg contains such a chromosome and only half the sperms do, is a difference explained by the method of origin of eggs and sperms, which needs no explanation here. If an egg fuses with a sperm containing an *X* chromosome, thus bringing two *X* chromosomes into the fertilized egg, the result is always a female (Fig. 54). If, on the other hand, an egg fuses with a sperm that does not contain an *X* chromosome, thus bringing only one such chromosome into the fertilized egg, the result is invariably a male (Fig. 54). Since the chances are about even that sperms with and without *X* chromosomes will pair in about equal numbers with eggs, the result is that approximately about the same number of males and females are produced. It is evident, therefore, that the character of the sperm determines the sex of the progeny. Of course it is not understood why such a chromosome should determine sex, any more than why other chromosomes are concerned in determining other characters. So far as our knowledge goes, they are merely associated with the results that appear.

Not only should plant-breeders be acquainted with Mendel's law; with what is meant by unit characters; with the behavior of these characters in inheritance; and with sex determination; but they should also have some knowledge of parthenogenesis, which means the development of an individual by an egg which has not been fertilized. This phenomenon occurs both among plants and animals, and, among plants, at least, it occurs even among the highest forms. This would seem to indicate that it is entirely possible for the egg to proceed in the development of a new individual without the presence of a sperm. This often happens in nature, and it has been accomplished artificially by stimulating the unfertilized egg with chemical substances, or by some physical change. This situation may be understood easily when it is realized that a great many plants and animals of low grade have no sexual reproduction, but reproduce either by ordinary cell division, or among plants by what are called spores. Sexual reproduction was the very last form of reproduction to be introduced among plants, and it is known that eggs and sperms among plants were derived from spores. When an egg proceeds by itself to produce a new individual, it is simply doing what any spore is able to do, and, therefore, parthenogenesis is merely a case where an egg does what its ancestors always did. In other words, it is "harking back" to an old power. Among the plants under cultivation, therefore, it must not be a matter of surprise that now and then good seeds are developed in the entire absence of pollen, and such seeds, of course, breed as true as though reproduction were by grafting or slips.

SUMMARY

A brief statement of Mendel's law is that when a hybrid reproduces, its progeny "splits" into the definite ratio 3:1; that is, three-fourths of the progeny resemble one of the parents of the hybrid, and one-fourth resemble the other parent.

Involved in this law is the idea of *unit characters;* which means that characters retain their individuality, being transmitted intact, and not blending with other characters. When two characters are mutually exclusive, one of them is always *dominant* over the other, which is then said to be *recessive.*

When hybrids are produced from parents that differ in some contrasting character, as color of flowers, all the hybrids will exhibit the dominant character; that is, they will all look alike, so far as this character is concerned. But when the hybrids reproduce, the Mendelian ratio appears.

The Mendelian ratio is often expressed as 1:2:1, indicating that three kinds of individuals are involved, although superficially only two kinds, in the ratio of 3:1, seem to appear. The three kinds are forms resembling each parent of the hybrid, and these forms breed true, having been really segregated from the hybrid mixture: while the third kind comprises forms that contain the hybrid mixture, and in subsequent generations continue to split in the Mendelian ratio.

The explanation of this behavior of unit characters is that paired characters received from the two parents are segregated in the germ cells (eggs and sperms), so that each germ cell contains only one of the characters. In such a case there would be two kinds of eggs and sperms, and the chance of mating is expressed by the Mendelian ratio.

The application of Mendelism in practical plant-breeding is in the intelligent handling of unit characters in producing new forms; in understanding the limitations of hybrids; and in suggesting a strictly scientific technique for experimental plant-breeding.

CHAPTER IX

RECENT WORK IN GENETICS

Any account of plant-breeding which stopped with a definition of Mendel's law and a description of the cytological machinery would be very incomplete. The conditions which Mendel met were comparatively simple. At least they were restricted to a single plant, so that the wider range of conditions was not observed. Mendel's law has been verified repeatedly in a remarkable way, but in connection with the investigations it has provoked, there has been a great extension of our knowledge of the conditions of inheritance. New situations have developed which were not observed by Mendel, and most of these situations have a direct bearing upon plant-breeding. The whole subject of Mendelism has become so very complex that it would be impossible for the general reader to understand it, but there are certain extensions of our knowledge of the subject that should be presented. Perhaps even more work has been done with animals than with plants, but our illustrations will be restricted for the most part to plants.

Very early in the development of genetics there was felt to be a need for terms to express certain situations. The list of special terms has become a long one, but there are a few which will be convenient in this discussion, and especially in any further reading upon the subject. In defining Mendel's law in the last chapter, it must have been obvious that the formula 3:1 is a formula for the appearance rather than for the constitution of the plants. For example, in the illustration used, a purple-flowered pea was crossed with a white-flowered form, and in the F_2 generation there were three purples to one white. At the same time, the constitution of these three purple forms was not the same. One of them had received the purple character from both parents; while two of them had received the purple character from one parent and the white character from the other. Bateson proposed the terms *homozygote* and *heterozygote* to distinguish these two kinds of constitution. The homozygous plant is one that has received the same character from both parents; while a heterozygous plant has received a different character from each parent. In our illustration, therefore, the pure purple strain is homozygous, while the mixed purple and white strains are heterozygous. To further illustrate the situation, it is evident that the plants of the F_1 generation are all heterozygous, and those of the F_2 generation are one-half homozygous and one-half heterozygous.

There are two other terms which will be useful in clarifying ideas. It will be remembered that Mendel's law really depends upon what is called the purity of the sexual cells (gametes); that is, each gamete contains only one of two contrasting characters, although both of them may have existed in the individual producing the gamete. If two pairing gametes contain the same character, the resulting individual will receive the same character from both parents, in which case the character is said to be *duplex;* that is there is a "double dose" of this character. The sexual cells from such an individual will all be alike so far as this character is concerned. On the other hand, if two pairing gametes contain contrasting characters, the resulting individual will have the dominant character from only one parent, in which case the character is said to be *simplex;* that is, there is a "single dose" of this character. The sexual cells from such an individual will be of two kinds, one kind containing the dominant character, and the other kind the recessive. If both parents are duplex in a given character, all the progeny will exhibit this character through successive generations; in other words, it will come true indefinitely so long as the progeny are interbred. If one parent is duplex and the other is simplex, the F_1 generation will all show the dominant character, but in the F_2 generation there will appear a certain number of individuals exhibiting the recessive character. If both parents are simplex, the F_2 generation will contain the characteristic number of individuals exhibiting the recessive character.

Davenport's illustration of eye pigments will serve to indicate how various situations may be analyzed. Brown pigment is dominant over blue, so that the children of two brown-eyed parents should all have brown eyes, but if blue eyes appear among the grandchildren, the inference is that in one or both of the grandparents the character was simplex. In this way the general pedigrees of plants and animals may be inferred and mixtures may be detected.

The best illustration of recent work among plants may be obtained from the extensive scientific breeding of maize, the results of which have been summarized by East.

Naturally the first work with maize was to verify Mendel's law, and to discover whether maize behaves in the same way as garden peas. It will also be of advantage to the reader to review Mendel's work in connection with this new form. There are two conspicuous strains of maize, namely starchy and sweet. It is found that the latter condition results from inability of the plant to mature starch grains. The sexual cells (gametes) of the two strains differ, therefore, according to Mendel's law, in that the gametes of one strain contain the starch-forming determiner, and the gametes of the other strain contain no such determiner. It is not a question, therefore, of two contrasted determiners, one of which, is dominant over the other, but it is a question of the presence and absence of a determiner.

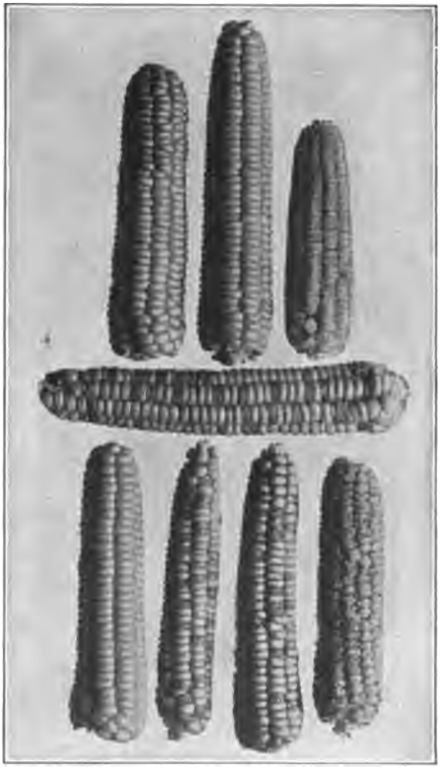

FIG. 55.—Behavior of starchy and sweet strains in maize: at top, the parents (right and left) and the F_1 generation (middle); in center, a single ear of the F_2 generation; at bottom, the F_3 generation.—After EAST.

In such a case, of course, the presence of a determiner is always dominant over its absence. In his experimental work, East discovered that a cross between two starchy strains resulted in a pure starchy strain; that a cross between two sweet strains resulted in a pure sweet strain; but that a cross between a starchy and a sweet strain resulted in a hybrid strain that behaved according to Mendel's law. This means that all the individuals of the F_1 generation (hybrids) were starchy, and that in the F_2 generation starchy and sweet individuals occurred in the proportion of 3:1. Of course, the three starchy individuals differed among themselves, one being homozygous and the other two being heterozygous (Fig. 55). In this case, as the figure shows, the three different kinds of individuals belonging to the F_2 generation are apparent.

East further tested this ratio by making an actual count of 30,000 individuals in the F_2 generation resulting from a cross between starchy and sweet individuals. The actual count gave 23,529 starchy plants and 7,811 non-starchy plants, which is a ratio of 3,0031:0.9969, which is near enough the ratio of 3:1 to be within the limit of possible error.

Similar work with very many plants for many kinds of characters has shown the same results in most cases. For example, the transmission of color characters has been an easy subject of investigation, which has now included over thirty species of plants. The transmission of structural characters has also been investigated, as, for example, tallness and dwarfness, hairiness and smoothness, bearded and beardless wheat, much-toothed and little-toothed leaves, and even two-celled and many-celled fruit (tomatoes).

In most cases of crossing among plants and animals, the conditions are by no means so simple as in the case of Mendel's peas or East's maize. In these more complicated cases the results appear to be different, and the 3:1 ratio is not evident in the F_2 generation, It is not understood clearly what complications are present that obscure the result, or that seem to modify the application of Mendel's law. The most numerous and obscure complications occur in the human race, so that the attempt to apply strictly Mendel's simple ratio to all human characters leads to confusion.

A very interesting situation arises now and then that deserves mention. We have explained the definite ratio of Mendel's law by the complete purity of gametes, that is, when gametes are produced, the contrasting characters are segregated, so that each gamete has only one of them. In East's experiments, however, there were cases in which pure types, separated from hybrid mixtures by breeding and which ought to have bred pure individuals, failed to do so. For example, among thousands of non-starchy seeds breeding true, after being extracted from the hybrid mixture, East found one occasionally which was semi-starchy and bred true to that character. In trying to explain such a situation there seem to be two alternatives: either the segregation of characters in the gametes was not complete, so that some gametes were not absolutely pure, or else the character for starchiness in the course of several generations was formed anew and became partially dominant. Future work ought to be able to determine which of these two alternatives is the real explanation.

Unless some more complicated case than that of such simple hybrids as we have mentioned is described, there would be danger of serious misapprehension as to the simplicity of heredity. There need be no attempt to consider extreme complications, many of which are too difficult even for students of genetics to analyze as yet. The next step toward complication will illustrate what difficulties arise as one proceeds from simple crosses to complex ones. Sometimes what seems to be a simple character is the result of the interaction of two factors. For example, in his experiments with maize, East found that the purple color shown by certain grains is produced only when two complementary factors are brought together in crossing. The way in which this fact came to notice is interesting, and illustrates the methods in genetics. A purple race of maize, when crossed with certain white races, resulted in purple hybrids, as would be expected, which split up in the F_2 generation in the usual ratio of 3:1. If these were the only experiments with the two races concerned, purple would seem to be a simple character. However, in crossing the same purple race with other white races of maize, a very different ratio was obtained. By analyzing the situation through breeding, it was discovered that the purple is not a simple factor, but is produced by a combination of two complementary factors. To procure the ratio of splitting in such a case it is necessary to multiply the simple ratio 3:1. In the case just given, the ratio turns out to be 9:3:3:1. This means that out of sixteen individuals, nine would be purple, because there would be just nine chances out of sixteen that the two purple factors would meet; and that one individual out of sixteen would be white; and that the remaining individuals would be mixtures.

A very important fact in connection with the existence of what may be called complementary factors is that they explain what has long been called *latency,* for latency evidently results from the fact that two complementary factors become separated in breeding, and so the character disappears, and never reappears unless two individuals bearing the complementary factors happen to be crossed. A very interesting illustration of this is obtained from the result secured by Bateson in his cultures of sweet peas. In crossing two cultivated races with white flowers, the hybrid generation secured was purple-flowered, the color of the wild race of sweet pea. This simply means that in cultivating races of sweet peas and separating white-flowered forms, the two factors producing purple were separated and when they were brought together in crossing the purple reappeared. Of course, it seemed a mystery to most people that crossing two white races resulted in a purple one. The same result was obtained by East in connection with the purple race of maize mentioned above, in which purple was found to be, not a simple character, but one produced by a combination of two complementary factors. These factors had become separated in breeding, so that the purple color had disappeared; but upon crossing two white races, the purple color reappeared (Fig. 56).

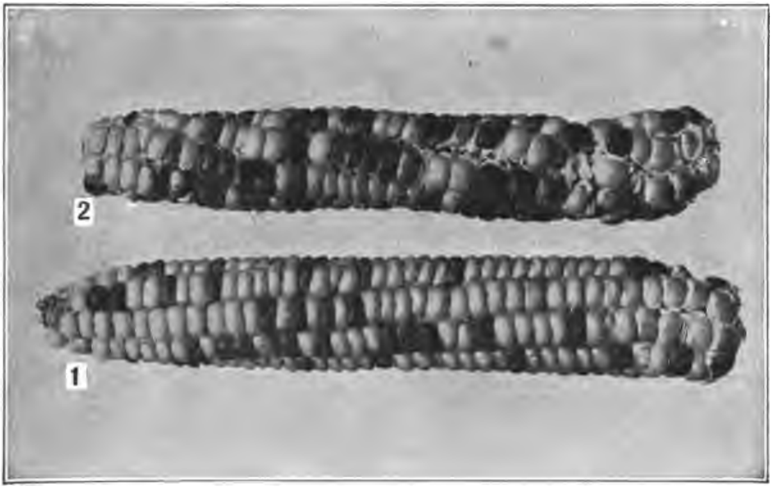

FIG. 56.—Purple seeds produced by crossing white seeds.—After EAST.

In addition to complementary factors, there have also been discovered factors that are coupled with one another and are transmitted together, and also factors that are antagonistic to one another, a term which explains the result. A case of coupling of factors has been shown by Emerson's experiments with maize.

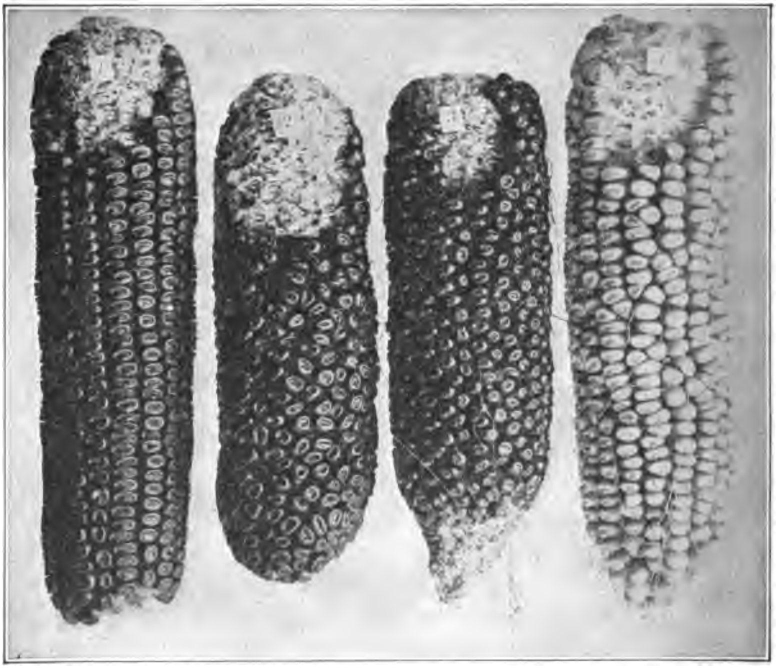

FIG. 57.—Red cob and seed coupled in inheritance (F_2 generation): ears *1, 2, 3* with red cobs and seeds; ear *4* with white cob and seed.—After EAST.

There are races of maize with red cob and red seed. In breeding such races and crossing them with races of no color, either in cob or seed, it appears that the red factors for the cob and for the seed are usually handed down together, that is coupled (Fig. 57), but they may be separated experimentally so as to show they are

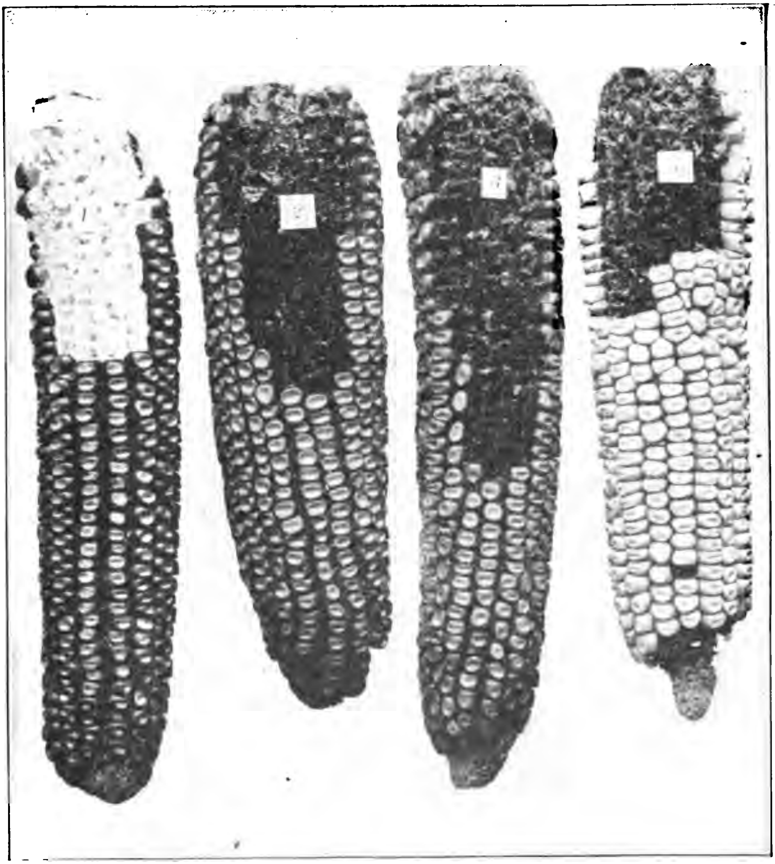

FIG. 58.—Red cob and seed separated in inheritance (F_2 generation): ears *1* and *4*, like parents, are pure types; ears *2* and *3* are heterozygous.—After EAST.

really two factors coupled together, and not one factor. Emerson produced races with red seed and white cob, and vice versa (Fig. 58), showing that these two features are not necessarily linked together.

There are also cases of what are called *blends,* which may result either from incomplete dominance or from the absence of any dominance. For example, it happens in the crossing of certain purple and white races of maize that the hybrid progeny has pinkish grains, which means an incomplete dominance of the purple. The classic illustration and the best one of blends is obtained from Andalusian fowls. There is a blue type of this race of fowls that never breeds true, and of course remained for a long time a puzzle to poultry fanciers. It was found that if two blue fowls were mated, only one-half of the progeny was blue, one-fourth being black, and the other fourth splashed white. The black and white strains breed true, and when black and white strains are crossed all of the progeny are blue. This led to what was called the paradox in the case of this inheritance, namely, that black crossed with white produces twice as many blues as blue crossed with blue. This simply means that blue is not a character represented by a determiner, but appears only by bringing black and white together with no dominance of either.

These are simple illustrations of the complications that arise, so that, although the fundamental law of heredity is simple, the interpretation of many cases becomes difficult.

SUMMARY

Mendel's experiments dealt with very simple problems of inheritance, so that the more complex situations were not realized when his law was formulated. The more recent work in genetics has included complex situations, and as a result the application of Mendel's law has often become so complex as to elude those who are not professional students of genetics. In a general way, however, the confirmation of Mendel's law has been remarkable.

The advance in genetics required the development of a special vocabulary to indicate situations clearly and tersely. Among the terms introduced, perhaps the most used and most useful are *homozygous* and *heterozygous,* the former referring to an individual that has received the same character from both parents, and the latter to an individual that has received from each parent a character contrasting with the other. The two individuals appear alike in reference to the given character, for the dominant will express itself, but they are very unlike in their breeding capacity.

In connection with the development of genetics new situations have been discovered as follows: the occasional reappearance of a character which has been eliminated by separating a pure line from a mixture; the occurrence of characters that are not strict unit characters, but depend upon the interaction of complementary factors, often producing unexpected results, and accounting for much of the so-called latency of characters; the occurrence of coupled characters that are usually transmitted together, but may be separated by breeding; the occurrence of antagonistic characters, which neutralize one another; and the possibility of blends, which may mean incomplete dominance or the entire absence of dominance.

CHAPTER X

COMBINATION OF CHARACTERS

A very old method of obtaining desirable plants is by means of artificial hybrids. In this way it is possible to obtain combinations of characters which do not appear in any pure strain. This work involves special skill in technique, for it means not only hand pollination, but also pollination at exactly the right time, and a careful guarding of the treated plants from foreign pollen. It is perhaps easy to recognize the proper condition of the pollen, for it is in condition to do its work when it is being shed by the anthers; but to recognize the proper condition of the stigma is not so easy. This receptive surface must be excreting its characteristic nutrient solution for the pollen grains, so that if pollen is applied either before or after this period it is of no avail. Naturally, therefore, only those plants can be crossed whose pollen and stigmas are ready at the same time. Even when the time relations are appropriate there is great diversity in the potency of pollen upon a given stigma. To secure successful crosses, therefore, involves more technical skill and knowledge of plants than is generally supposed.

When the crossing has been effected and a generation of hybrids secured, it does not follow that all of the hybrid individuals will show the desired combination. If a plant-breeder uses a small number of hybrids he may work for a lifetime without securing the desired combination. If he uses hundreds of hybrids he is more likely to secure the combination sooner or later. If he uses thousands of hybrids he may be almost sure that one or more of them will show the combination sought for. In other words, the bare chance of securing a combination can be changed into reasonable certainty if the number of hybrids is large enough. It is this use of very large numbers that has brought such a great measure of success to the various combinations sought for by Burbank. Our best illustration as to what can be done in plant-breeding by the use of hybrids can be obtained from his work.

There is a wild blackberry which has a white or cream-colored fruit of peculiar flavor, but it is very small. The well-known Lawton blackberry of cultivation is large and black. Burbank conceived the idea of combining the color of the wild berry with the size of the cultivated berry. The necessary crosses were made and, among the thousands of hybrid individuals produced, one or more showed the desired combination. Such an individual was used for propagation and a race of large white blackberries was established.

The seedless apple has become rather famous, but it was secured in just the same way. There have always been seedless apples, but they have never been of good quality. Burbank crossed a poor seedless apple with an apple of good quality, but containing seeds. Among the numerous hybrid individuals produced this combination was at last secured, so that now there are seedless apples of fine quality.

Perhaps as well-advertised a case of hybridizing as any that has been performed is that which resulted in the so-called spineless cactus. In the arid regions inhabited by the various species of cactus it would be of great advantage if the cactus could be used as a forage plant for stock. This, however, is said to be impossible on account of the spines which make cactus plants unapproachable. At the same time, those cactus forms known as the prickly pears are very succulent, and would be very useful for forage if the spines did not prevent. All kinds of cactus produce occasional individuals that are relatively spineless, and in some species these individuals are quite common. Those species, however, that show numerous spineless individuals are not succulent, and therefore are of no use as forage. The problem which Burbank set for himself was to combine the spineless character of the useless cactus with the succulent character of the very spiny prickly pear. It was a difficult piece of technique, but was finally accomplished, so that now a race of spineless cactus is announced as a forage plant suitable for arid

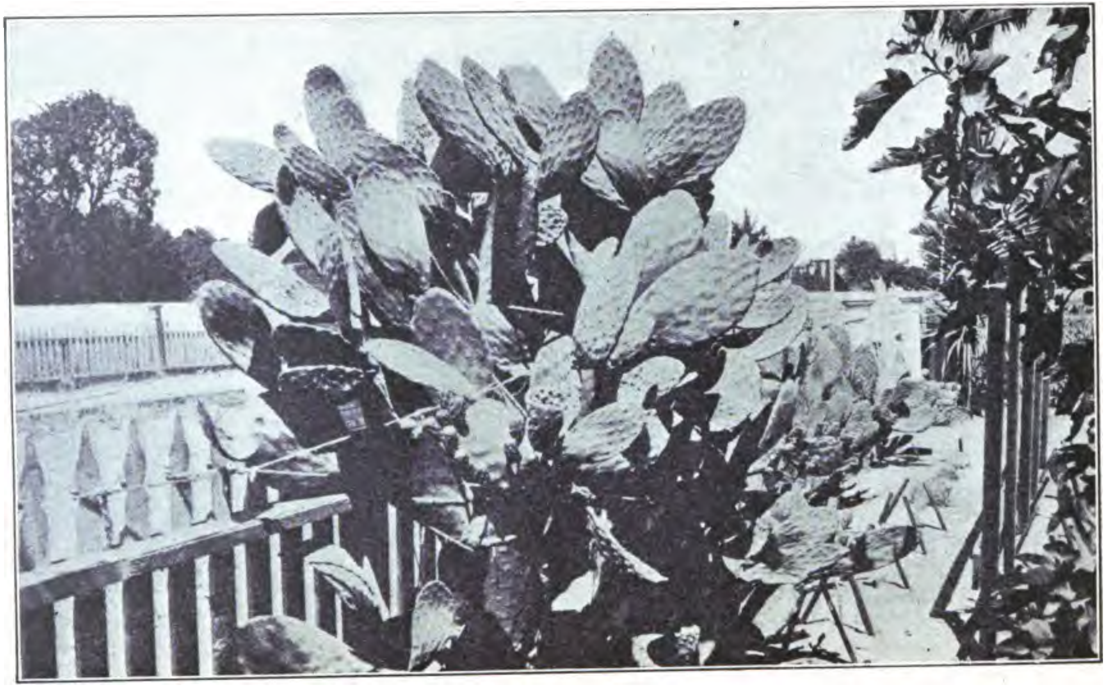

Fig. 59.—The spineless cactus.—After DeVries.

regions (Fig. 59). The range of conditions in which it will grow is somewhat limited, so that its exploitation beyond this limited range is commercial rather than scientific.

In these cases, which may serve as illustrations for a great many, it should be recognized that no new principle is involved; that there is no mysterious elimination of color, and seeds, and spines, but that the use of large numbers of hybrids, coupled with great skill in the technique of hybridizing, secured the results that were to be expected. Another fact in connection with these hybrids, or any others, is that they are subject to the operation of Mendel's law, and therefore must split up in each generation, provided they are propagated by seeds, which, of course, involves sexual reproduction. In such a case, therefore, if two relatively undesirable parents are crossed and a desirable hybrid secured, in subsequent generations half of the plants will represent the undesirable parent forms, and only half will continue the desirable hybrid. It will be noticed, however, that the hybrids mentioned, and most others produced for permanent use, are of plants that can be propagated vegetatively. The white blackberry and the spineless cactus, and of course the seedless apple, do not need to be reproduced by seeds, but by cuttings or grafting or vegetative multiplication of some kind.

It is possible to secure not merely ordinary hybrids, but what are known as triple hybrids, by combining three different races or species. This, of course, calls for a much higher development of technique than ordinary hybridizing. The most notable illustration of this is Burbank's Shasta daisy, in which he has secured a combination of characters belonging to three distinct parent stocks: the American, English, and Japanese. The characters combined in this triple hybrid are interesting. The American daisy, or marguerite, is a very free bloomer, but with an undesirable type of body, the stem having a sprawling habit and the leaves not being attractive. Its English relative has an attractive body, the stems standing erect and producing handsome leaves. The Japanese form has flowers with a remarkably attractive pearly luster. Burbank sought to combine in one plant the profuse blooming of the American form, the stately carriage of the English form, and the pearly luster of the Japanese form, and the result was the Shasta daisy (Fig. 60). This kind of hybrid is apart from our present purpose, but it illustrates what may be possible in connection with plant-breeding after we have accomplished all that ordinary hybridizing can do. Another interesting fact in reference to the Shasta daisy is that it is propagated by seeds, and apparently is not showing the ratio of splitting called for by Mendel's law.

The most important fact in connection with hybridizing remains to be told. It is useful to secure a combination of desirable characters, but it is necessary to secure

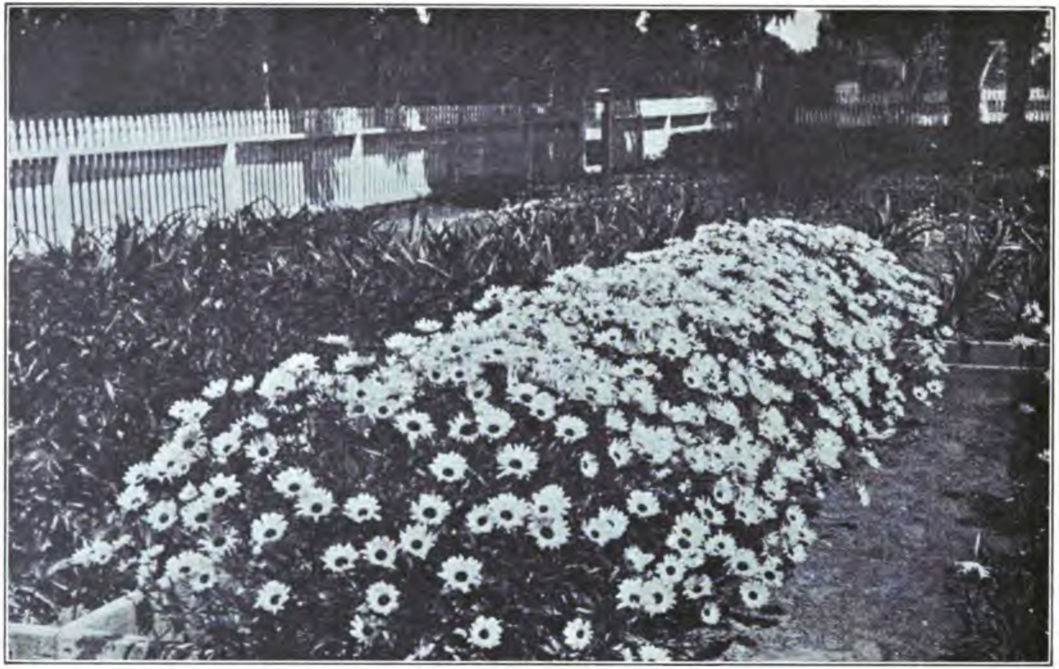

FIG. 60.—The Shasta daisy.—After DEVRIES.

as great vigor and yield as possible, and this stimulus to vigor is a common effect of hybridizing. It is true in general that a hybrid plant grows more rapidly and becomes larger than either parent. Burbank secured this in a striking way in crossing an American walnut with an English walnut, and as a result has produced a hybrid walnut that grows much more rapidly and becomes much larger than either of the parent forms (Fig. 61). He also crossed the California dewberry with the Siberian raspberry, both of them species belonging to the same genus, and both of them comparatively worthless as berries, and secured among the hybrids fine and vigorous plants with large berries.

This same fact has been discovered in connection with corn-breeding. A cornfield is the most extreme mixture of different kinds of individuals represented by any one of our field crops. This means that the ordinary commercial maize is a mixture of a great many strains or races. When these races were separated from one another by pedigree culture and pure strains were thus secured, it was found that the individual plants deteriorated in vigor in proportion to the purity of the strain. This deterioration went down to a certain fixed level, which represented the natural vigor of each strain, and which was very inferior to the ordinary plant of the mixed fields. By crossing any two pure strains a much more vigorous plant was obtained. This situation is illustrated roughly by the results of self-

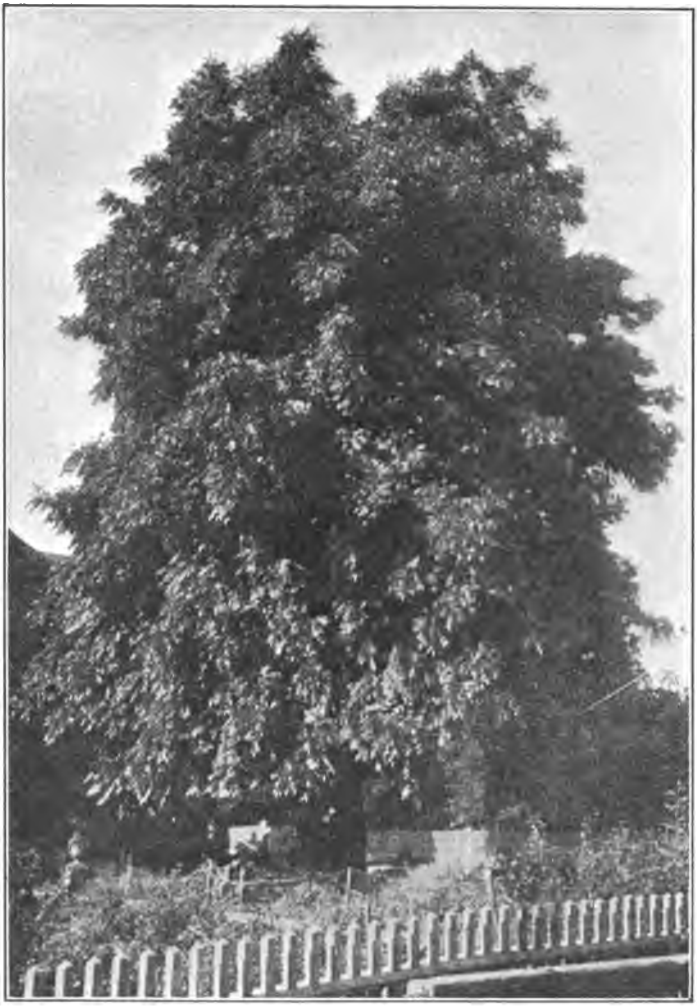

FIG. 61.—A hybrid walnut, double the height of ordinary trees.—After DEVRIES.

pollination and cross-pollination in maize. The cross-bred plants grow much more rapidly and vigorously than do the close-bred plants (Fig. 62). Hybridizing, therefore, is a stimulus both to the rate and amount of growth. Another way of stating this fact is that the more unlike the two parents are, the more extreme does the stimulus of growth become. Vigor may be expected then to come from dissimilar parents, and this has been found to apply to the human race as well as to plants.

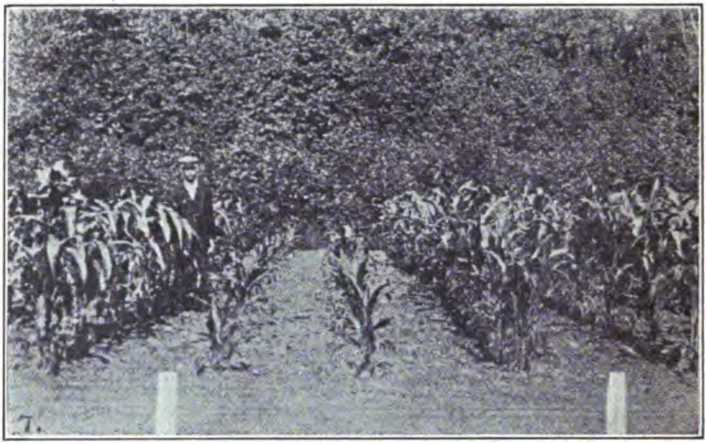

FIG. 62.—Rows of maize showing effect of close and cross-pollination, the two rows of short plants (in center) resulting from close pollination.—After DEVRIES.

The question is often raised as to the possible range of hybridizing. Of course it is a common experience of the plant-breeder to cross closely related strains or races, and also to cross what are known as related species, but can genera be crossed, or even more distantly related plants? This question has not been answered fully, but certain genera have been crossed, and the limit of crossing has yet to be discovered. It must not be supposed that there is any definite boundary line for crossing within which any forms can be crossed. Plants are exceedingly variable in this regard. In some genera all the species will cross freely, while in other genera certain of the species will not cross at all. Even races of the same species may refuse to cross. The possibility of crossing suggested by relationship must always be tested experimentally before there is any assurance that crossing is possible. There can be no doubt but that there has always been an immense amount of crossing in nature, and it is probably true that the vigor and tone of plants depend upon free crossing of different kinds. It is probably true that permanently new forms have been produced in this way, as well as by natural selection, mutation, or orthogenesis.

Another use of hybridizing is beginning to be developed, and will certainly prove of very great importance. Not only can it be used to secure a desirable combination of characters, and to secure vigor, but it can also be used to eliminate characters that are undesirable and destructive. One of the best illustrations of this use of hybridizing may be taken from the experiments of Biffen in England upon the English races of wheat.

The English wheats have been brought up to a high state of productiveness, so that the productive power is perhaps as high as that of any other wheats that are grown. At the same time, this high productive quality has become associated with the destructive rust disease. In other words, these high-grade wheats are peculiarly susceptible to this disease. While the rust does not destroy the wheat plants, its presence deteriorates the quality of the grain, so that the grain secured from rust-infected plants makes a very inferior bread. Biffen searched through various countries for strains of wheat resistant to rust, and he found them, but they were races with a low yield. What he did, therefore, was to seek the combination of the rust-resistance of the poor wheat with the high quality of the susceptible wheat, and this he secured in a very complete way, so that now we have in England races of wheat of high yield and quality, and at the same time rust-resistant. In this case, since wheat is propagated by seed, this desirable hybrid must reckon with Mendel's law. As will be seen later, hybrids are said to be "fixed," which does not mean that they do not split, but means that the average of the crop is desirable. If the seed is carefully selected each generation, the undesirable forms can be eliminated until the average of the crop is very high. Of course it will always contain undesirable individuals, representing the original parents of the hybrid.

Another illustration of the use of a combination of characters to eliminate undesirable ones may be obtained from the work of Webber and Swingle on citrus fruits. As is well known, the great enemy of the orange-grower in Florida is the occasional frost, just as the occasional drought is the great enemy of the maize-grower. The problem that Webber set for himself, therefore, was to secure, if possible, a frost-resistant

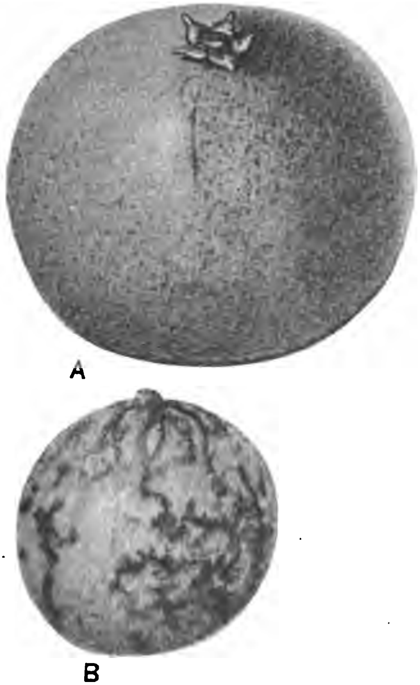

FIG. 63.—*A*, frost-resistant orange ("rusk citrange") produced as a hybrid; *B*, the hardy, trifoliate orange used in producing the hybrid.—After Year Book, Dept. Agri.

orange. In his experiments he crossed the ordinary orange with a well-known but useless hardy form. Among the hybrids produced he secured, not merely a combination of good quality and frost-resistance, but several very desirable varieties on account of their peculiar qualities (Fig. 63). He reports that the trees of three valuable varieties produced have endured a temperature of 8° F., and the statement is further made that through this kind of work the orange culture can be extended four hundred miles north of its present range.

SUMMARY

The uses of hybrids in plant-breeding are numerous, and the successful practice of hybridizing requires great technical knowledge and skill.

Perhaps the most important use of artificial hybrids is to secure a combination of desirable characters which does not exist in any plant. The desired combination may appear only in one individual among thousands of hybrids, so that very large numbers must be used to insure success. It is this combination of characters that has chiefly characterized the work of Burbank.

The most successful hybrids are those that can be propagated vegetatively, since reproduction by seeds, involving the sex act, introduces the Mendelian ratio of splitting, so that not more than one-half of the crop maintains its hybrid character.

Another use of hybrids is to secure greater vigor and more rapid growth. What may be called the stimulating effect of hybridizing is very marked, so that in many cases the best crop plants are those that have been intelligently crossed.

A third use of hybridizing is to eliminate undesirable characters, as susceptibility to diseases, to drought, to cold, etc.; resistance to these dangers being combined with the desirable qualities of susceptible plants.

The possible range of hybridizing is not limited by natural relationship. Even genera have been crossed; but, on the other hand, closely related species, and even races of the same species, may not cross.

CHAPTER XI

THE RÔLE OF HYBRIDS

In the preceding chapter the use of hybridizing in securing desirable combinations and qualities was considered. This gives one view of hybrids, and Mendel's law gives another. Hybrids enter so much into all considerations of heredity and plant-breeding that a general consideration of their nature and their practical applications will be helpful.

Since the discovery of Mendel's law, which teaches that hybrids split in such a way that not more than one-half of their progeny show the hybrid character, there is danger that the usefulness of hybrids in plant-breeding will be too much discredited. It is the purpose of this chapter to indicate the important rôle played by hybrids. It must be recognized that hybridization is the most important method of securing variations artificially. There are endless variations in nature, but man can deliberately add to these variations by crossing two kinds of plants, the resulting hybrid being an artificially produced variation. Doubtless many variations observed in nature are natural hybrids, but man can add to them artificially. Not only may variations in general be multiplied in this way, but definite combinations of characters can be secured, which may be regarded as planned variations. Such variations would never occur in nature, and yet they are often enormously useful. The only other important method of securing variations is to catch them as they appear naturally, and "fix" them.

The term "hybrid" has had different applications. At first it was restricted to the progeny arising from the crossing of parents belonging to two different species. Since that time, however, the species concept has not only become more vague, but it has also been split up into such minor categories as varieties, races, strains, forms, etc., all of them expressing degrees of difference. As a consequence, a hybrid has come to mean the product arising from the crossing of two distinctly different parents, whether they represent strains or races or varieties or species or even higher categories of classification.

As has been stated, there is no fixed rule as to the possible range of crossing. In general, the possibility of successful crossing increases as the parents are more nearly related, but even apparently closely related species or races may prove to be incapable of crossing, so that the plant-breeder must test each proposed cross as to its possibility. In some genera the species cross freely, while in other genera they may cross with difficulty or not at all. In some cases representatives of different genera may be crossed, as has been done with wheat and rye, wheat and barley, strawberry and raspberry, tobacco and petunia, etc. There are also recorded cases of crosses between representatives of different families, but this is so very rare that it cannot be regarded as of any practical importance.

The first recorded plant hybrid was made by Thomas Fairchild, an English gardener, early in the eighteenth century. He crossed carnation and sweet william, and this hybrid was under cultivation for more than a century, and possibly is still cultivated. The reason why the crossing of plants lagged so far behind the crossing of animals is that the sexuality of plants was not recognized until the close of the seventeenth century, and it was nearly a century later before advantage was taken of this knowledge in any extensive way.

As has been said, there is no doubt but that there is extensive crossing of plants in nature, and that this is partly responsible at least for extreme variation among plants. It must be remembered, however, that plants differ widely as to the chances of crossing. Some plants are constructed for open pollination, as maize, and as a result a corn-field shows greater variation among individuals than is shown in a field of any other cereal. On the other hand, the domesticated races of wheat are constructed for close pollination, and there is much less variation among individuals. This relation between open pollination and variation, and between close pollination and relative constancy is probably not appreciated fully. Open pollination results in multiplying mixed races, while close pollination is natural pedigree culture. When plants are cultivated upon such a scale as to make protection against cross-pollination impracticable, as in the case of all our important field crops, the adjustment of plants for cross or close pollination is a very real factor in the problem of constancy.

To secure a hybrid means artificial cross-pollination. In general the method used is as follows: The anthers must be removed from the flowers to be artificially pollinated before they have become mature enough to shed pollen. Usually the flower bud is opened carefully and the anthers are removed, either by cutting them off, or by pulling them off, depending upon the structure of the stamen. In horticulture this process is called *emasculation.* The emasculated flower or cluster of flowers is then inclosed in a loose bag to prevent chance pollination. When the stigmas are mature, or in the condition to receive pollen, the selected and shedding anthers are rubbed on the stigmas, or the pollen may be transferred from anther to stigma by a fine brush. The treated flowers are then bagged again to prevent access of undesirable pollen until fertilization has been accomplished. Plants vary widely as to the ease with which artificial pollination can be accomplished. One must learn this technique as any other delicate technique, which involves not only skill in the emasculation and the transfer, but also in the recognition of the proper condition of the stigma.

When desirable hybrids are produced which can be propagated vegetatively by tubers, bulbs, cuttings, grafts, etc., they breed true without further care. It is doubtless true that such hybrids are to be regarded as the most valuable. When they must be reproduced by seeds, however, as in the case of cereals, they must be "fixed." This process consists in self-pollination ("inbreeding") and careful selection of the most desirable individuals through several generations. When this process is analyzed on the basis of Mendel's law it is evident that there is no such thing as "fixing" a hybrid in the sense that all of its progeny will breed true. Close pollination guards it against mixture with inferior forms, and continuous selection increases the desirable characters, but the hybrid must split, and the total result is not to secure a uniform progeny, but to secure a good average. The progeny will be a mixture of forms, approximately one-half of which are not hybrids at all. In spite of this, to produce a high average in such crops as cereals is very important.

The advantages in producing hybrids are numerous, and the principal ones are as follows: It is clear that hybridizing may be used to secure desirable combinations of qualities which are not found in existing plants, as described in the preceding chapter. In addition to anticipated combinations, a great range of unlooked-for variations may be secured, some of which will be found desirable. Such results are perhaps more important in floriculture than in any other form of plant-breeding. Frequently the characters of the two parents remain so distinct that the hybrid appears as a sort of mosaic combination of the two.

A striking feature of many hybrids is their vigor as compared with that of the parent forms. In such cases crossing seems to act as an extra stimulus to growth, both in rate and amount. For example, Burbank's hybrid walnut tree (Fig. 61), a cross between the Californian black walnut and the English walnut, already cited, is remarkably larger than either parent. It is reported that this hybrid grows twice as fast as the combined growth of both parents. In crossing the western dewberry with the Siberian raspberry the hybrid ripens its fruit several weeks before either of its parents and exceeds them remarkably in productiveness and largeness of fruit. The case of maize, mentioned in the preceding chapter, is a further illustration of this effect of crossing. It will be remembered that as pure strains of maize are extracted from the usual mixture of individuals they deteriorate in size and vigor to a certain level, but when two pure strains are crossed the result is the vigorous plant we are familiar with in fields of maize.

Tobacco is an excellent illustration of the increased vigor of a hybrid. The species in general are selfpollinated, so that under ordinary circumstances they must get along without the increased vigor due to crossing. In consequence of this the effect of artificial crossing shows a striking contrast. It has been found that the varieties of the common species (*Nicotiana tabacum*) when crossed produce hybrids 5 to 20 per cent. taller than the average height of the parents, and also with somewhat larger leaves. The same thing is true in general for crosses of varieties of other species. Sometimes there is a remarkable increase in vigor, one cross recorded by East resulting in hybrids double the size of the parents.

In such a country as the United States there is the greatest diversity of soil and climate, and in consequence many races of each kind of cultivated plant are demanded to meet all the varying conditions. For example, the best tomato in New York is totally unfit for Florida, and the same fact holds for almost every kind of cultivated plant. The plant-breeder is familiar with the fact that the favorite races in New England and New York are for the most part entirely different from those that do best in the South and West. For this reason any process which develops great variation increases the chances of securing plants suitable for each region. A few illustrations will suffice.

The oranges and lemons of Florida are occasionally destroyed by severe cold weather. This has led to enormous losses, so that nothing is more desirable for

Florida than hardy races of the citrus fruits. The plant-breeders of the department of agriculture have taken this need in hand, and have produced hardy races that should not only insure citrus culture in Florida, but should extend it. They used the so-called Japanese trifoliate orange, which has poor fruit but is hardy as far north as Philadelphia, and crossed it with the Florida oranges of good quality, and secured hybrids that had the combination of hardiness and good quality (Fig. 63).

The extension of various cultivated plants northward has been secured not only by selection, as has been mentioned in connection with the Canadian northward advance of wheat, but also by hybridization, by which hardier races and races of shorter season have been secured.

It is very desirable also to extend the cultivation of certain plants into warmer regions. For example, pear culture in the southern states was impossible until a combination with an oriental pear, the so-called Chinese sand pear, was secured. This showed the necessary vigor and resistance to a warmer climate, and with it as the hardy parent the high-grade pears were crossed and combinations secured that revolutionized pear culture in the South.

In many cases hybridization has resulted in securing races immune to destructive diseases, the character of immunity being furnished usually by a parent undesirable in other respects. The whole subject of disease-resistance will be discussed in a later chapter.

One of the very interesting phases of hybridization is included under the name *xenia,* a name given by Focke in 1881 to indicate the direct effect of foreign pollen. The best proved instance of the immediate effect of pollen is that of maize. For example, when a race of white or yellow maize is crossed with pollen from a race of red maize, many of the resulting grains are red or mottled. When this was reported, nearly two centuries ago, and continued to be reported from the experience of farmers and breeders, it was thought to be an impossible situation. The red pollen parent, it was claimed, might well transmit its color character to the embryo, and this character would reappear in the grains developed by the next generation, but that it should have an immediate effect upon the grain in which the embryo was forming seemed inexplicable. This has all been explained now by the discovery of what is called double fertilization in all flowering plants. Not only is the embryo a product of a fusion with a male cell, but the endosperm is also a product of a fusion with a male cell, and these immediate influences of the pollen parent are always shown by the endosperm. In this way it has become possible in several cases to get the characters of the pollen parent in the fruit of the pistillate parent. Of course, the use of the phenomenon of xenia may never be very extensive, but there are possibilities in it which have not yet been developed in plant-breeding.

SUMMARY

One of the effects of the extensive application of pedigree culture and of Mendel's law has been to discredit the use of hybrids as an important feature of plant-breeding. There are several important advantages in producing hybrids that should be realized.

A hybrid is not merely a product of the crossing of two species, but it includes all individuals produced by the crossing of unlike individuals, without reference to the closeness or distance of the relationship.

In spite of the great variations that appear naturally when plants are left to themselves, many desirable variations are not found in nature, and many that are very important would never occur in nature. It is only through artificial hybridizing that the full range of desirable variations can be secured.

Hybridizing plants began long after the deliberately planned crossing of animals, because the sexuality of plants was not recognized until the close of the seventeenth century.

The technique of artificial cross-pollination involves skill in the emasculation of the flowers to be pollinated; in the protection of the flowers from chance pollen; and in the transfer of pollen from stamen to stigma. Each kind of flower presents its own problems of technique.

Hybrids that can be propagated vegetatively breed true without further care; but those that must be propagated by seeds must be "fixed." Fixing a hybrid means that self-pollination is continued through several generations, accompanied by continuous selection of the most desirable individuals. The result is not an elimination of all individuals that are not hybrids, but an improvement of the average of the total population, so that the general result is good in spite of the admixture of relatively undesirable individuals.

An important use of hybrids is based upon the fact that they are often more vigorous and rapidly developing plants than either of the parents. As a supplement to the securing of pure strains by rigid pedigree culture these strains are crossed to secure vigor.

By means of hybrids strains best suited for different cultural conditions may be secured according to a well-defined method, which eliminates the necessity for a chance finding of a desirable race.

In many cases it is possible to secure disease-resistant races of desirable crops by crossing disease-resistant individuals with susceptible individuals of desirable quality.

CHAPTER XII

HOW TO SECURE DROUGHT-RESISTANCE

Drought is to be regarded as a constant menace to cultivated plants, especially to field crops which are too extensive to make an artificial water supply practicable. For this reason such important crops as wheat and maize are limited to regions of good water supply, and even in these regions an occasional drought is always to be feared. The losses from drought are numerous, and when this includes our fundamental crops the results are disastrous and far-reaching. Attention has been called to the fact that our population is increasing at a much greater rate than our food production. It is obvious that this discrepancy cannot be allowed to continue; in fact, the problem of food supply bids fair to become acute.

There are three lines of attack upon this problem which, taken together, should enable food production to overtake population. Plant-breeding should enable us to make plants more productive, to insure productiveness every season, and to extend production over areas not now under cultivation. Knowledge of the soil and its appropriate manipulation should enormously increase yield. Properly equipped men, trained in the technique of scientific agriculture so that they can secure for plants and soil the most effective relations to one another, should bring every region into its greatest productiveness. The problem is exceedingly complex, and no single achievement will solve it, but the recent development of plant-breeding has suggested the possibility of some important contributions toward its solution. Among these suggested possibilities, if plant-breeding can secure drought-resistant races of our more important crop plants, this would insure such crops against drought in regions where they are now cultivated, and would also extend enormously the area of possible cultivation. To say that this would at least double our present food production is perhaps a statement far short of the truth.

The principles of plant-breeding illustrated in the preceding chapters suggest the helpful procedure. The first thing is to discover whether there are in existence any drought-resistant races of the plants under consideration. Such forms may exist as wild plants in semi-arid regions, or they may occur as members of the mixed population usual in our cultivated fields. Even if complete drought-resistance is not found, a certain amount of resistance may be laid hold of and increased. The most hopeful search for drought-resistance is among the wild representatives of our domesticated races, for long cultivation in conditions of less exposure pampers a race of plants just as it does a race of men. For example, wheat has been in cultivation for thousands of years, and our domesticated races have become very susceptible to drought and disease. It has been found impracticable to make a pampered race hardy again, but it is entirely possible to maintain a hardy race. When drought-resistance in any degree is discovered it is necessary to learn through breeding whether this quality is inheritable and appears in each succeeding generation.

After drought-resistant forms have been found and pedigreed for inheritance, it will be necessary to consider quality. Our cultivated races have been brought up to certain standards of quality which must at least be maintained. It is altogether probable that the discovered drought-resistant form, especially if it be a wild form, will be inferior in quality. If it cannot be brought up to quality its drought-resistance will be of no avail, for quality is the first consideration. The problem is to combine drought-resistance and quality, and there are two ways of securing this. The hardy race may be brought up to standard quality by continuous selection, just as most of the domesticated races have been. This is necessarily a slow process, and complicated in this case by the fact that selection must be made, not only for quality, but also for drought-resistance. The other method is to cross the hardy race with races of good quality and thus secure the combination in a hybrid. It will be remembered that the desired combination will not occur in all the progeny, but if enough hybrids are produced the desired combination will be found. The disadvantage of this method arises from the splitting of hybrids, and if drought-resistance and quality behave as unit characters only one-half of the progeny of the hybrids would continue the desired combination. But even this result would be worth while, for the average result would be far in advance of any now secured by the domesticated races.

The subject of drought-resistance in connection with a crop of first importance has become conspicuous recently through the discovery of the wild original of wheat, which proves to be both drought-resistant and disease-resistant. An account of this discovery and its possibilities will illustrate not only what may be accomplished with wheat, but also what may be possible with other important crops.

Wheat is a crop of peculiar interest for several reasons. So far as we know, it was the first plant brought under cultivation. If this be true, it was very instrumental in changing the human population from wandering hunters to a settled agricultural people. To learn the region in which this plant was taken from the wild state and brought into cultivation, therefore, would be an important historical fact. Another interest attached to wheat is that it has been perhaps more influential in developing the principles of plant-breeding than any other plant. As a consequence of the long-continued work with wheat many races have been developed with varying qualities, and in connection with this work many principles of plant-breeding have been developed.

The wild original of wheat had been long sought for in vain, and the conclusion was reached that it had been under cultivation so long that the wild stock had disappeared. In searching for it the thought was that it would be an inconspicuous wild grass that through long cultivation had been brought up to its present condition.

Aaronsohn, a botanist of Palestine, had reached several conclusions in reference to wild wheat which are interesting because they led to its discovery. Everything seemed to indicate its origin in arid regions and its gradual removal into more humid regions. For example, it was known that when varieties from drier habitats were transferred to more humid habitats they were more vigorous than the varieties grown in humid regions. This would indicate that the plant naturally belongs to the drier habitats and becomes weakened in a humid environment. Conversely, it was found that varieties adjusted to humid existence do not succeed in drier regions. For example, wheat for our semi-arid regions is not obtained from our eastern humid races, but Durum wheat (hard wheat) from southern Russia, Turkey, and Asia Minor. The problem, therefore, was to find the native country of hard wheat.

The historical progress was from drier to more humid regions.

Aaronsohn also concluded that primitive men would not select a useless and inconspicuous grass for culti-

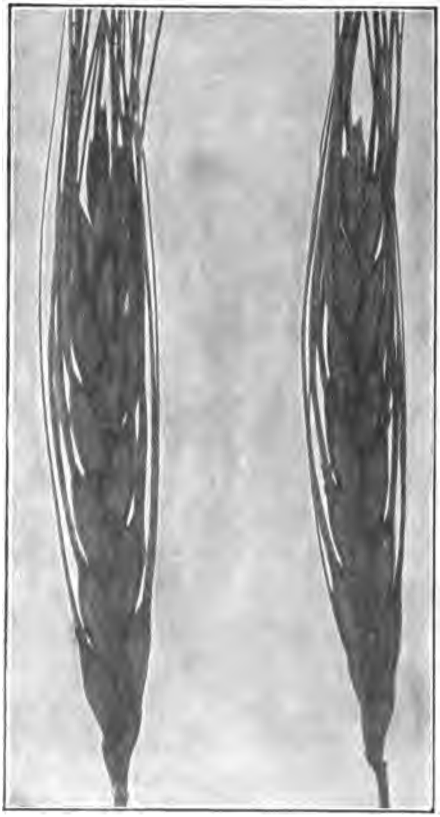

FIG. 64.—Nearly mature heads of wild wheat, ordinary form.—After COOK.

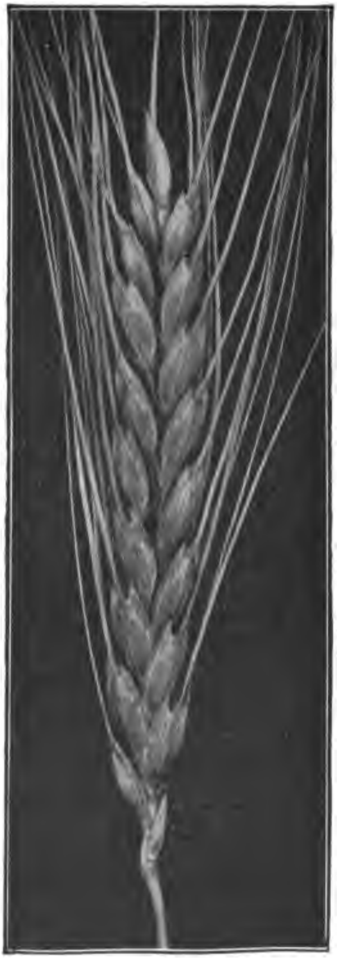

FIG. 65.—Head of a large-seeded variation of wild wheat.—After COOK.

vation, but would rather select one because it was already useful. It would call for too much insight in primitive men to have expected them to recognize the possibilities in an apparently useless plant. As Aaronsohn has put it, "It would have taken a wonderful power of divination on the part of our prehistoric ancestors to pick out one grass and to find out that this grass has such possibilities. We have done no such thing since with the thousands of other species of grasses."

Following this idea, Aaronsohn found wild wheat growing abundantly in Palestine as a grass fully as conspicuous as cultivated wheat. In fact, the heads are as large as those of cultivated wheat and the kernels are heavier (Figs. 64 and 65). "We must conclude that the cereals created civilization, and that civilization did not create the cereals." It is obvious that wheat has improved very little under cultivation. It is certainly true that the vigor of the plant has diminished very much, since it has become very susceptible to both drought and disease. Aaronsohn made the announcement of this discovery in 1906, the wild plants being found originally in the region around Mount Hermon. The wheat is a dominant grass over large areas, chiefly so rocky and broken as not to be fit for agriculture (Fig. 66). The first question to decide was whether this wild wheat was not merely an escaped form from cultivated fields that had established itself. All of the evidences for such a connection proved be-

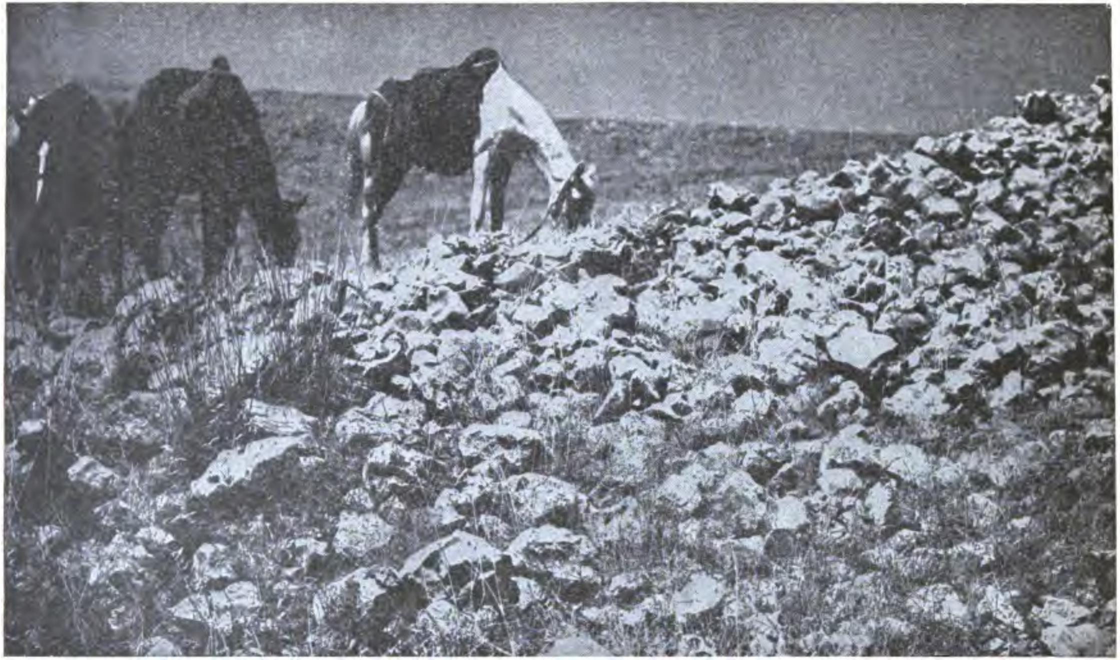

FIG. 66.—Wild wheat growing among nummulitic limestones in Palestine.—After COOK.

yond peradventure that this was really a wild wheat. Since the original discovery it has been found that the plant is widely distributed throughout Palestine and Syria, extending down the Jordan Valley to the Dead Sea. Its distribution shows that it is able to grow in a great variety of conditions, since it occurs from the top of Mount Hermon, which is often snow-covered, to the hot, dry cliffs of the Dead Sea Valley.

An interesting question is whether this Palestinian wheat is actually the original (prototype) from which the cultivated races were derived. The nearest approach to it in characters, including drought-resistance, are probably the wheats called "emmer" and "einkorn." At the present time, however, it is regarded as a distinct species and has been named *Triticum hermonis,* from the place of its original discovery. It is at least a wild relative of the forms from which the domesticated races were derived. Whether it be the actual prototype of our domesticated wheats or not makes no difference as to its importance. This is merely a question of scientific interest. The practical fact is that it is extremely valuable, and that it is related to the domesticated races so closely that it can be crossed with them.

Some of the features in which this wild wheat differs from the domesticated races may be mentioned. First and foremost, because perhaps most desirable, is its extreme drought-resistance. This will be appreciated better when it is stated that the conditions under which it occurs so abundantly are practically the same agriculturally as those of New Mexico, Arizona, and Southern California, which we recognize as semi-arid regions, incapable of use for any of our domesticated races of wheat. A second contrasting feature in which it is decidedly different from the domesticated races is its disease-resistance. Millions of dollars are lost annually from diseases that attack our pampered races of wheat, notably the rust diseases. The Palestinian wheat seems to be for the most part immune to rust, so that it is capable of insuring not merely against drought, but also against disease. Another important character is that it shows a wide range of variation, which means that under breeding methods it is capable of yielding many strains, suited to a great variety of conditions.

Perhaps the most notable biological feature of the Palestinian wheat in contrast with the domesticated races is the fact that it is cross-pollinated. Wheat has always been regarded as the chief example of a self-pollinating crop. This has made its improvement through selection a very simple process, a process which would not be possible with maize. Like most wild grasses, this wild wheat pushes out its stamens freely and the pollen is scattered by the wind (Fig. 67). The heads also show a most interesting adjustment to arid regions. In relatively moist conditions, as morning dew, the glumes spread apart and the scattered pollen reaches the inclosed stigmas, but when the heads become dry the glumes close again and the stigmas are protected against drying out. This wild wheat also matures grains through close-pollination, so that either method can be used. It seems likely that the domesticated races have happened to be derived from close-pollinating forms, and so this method has been continued as the only one with cultivated forms. The importance of this situation lies in the fact that cross-pollination gives a much greater range of variation, and as a consequence it would be possible to develop a much greater number of distinct races:

The application of this discovery to our own country will be that wheat crops may be insured against drought in regions where they are now cultivated, and in addition they can be cultivated in our semi-arid West and Southwest. This will enormously extend the yield of this fundamental food crop. In fact, the very peculiar method of dissemination of this wild wheat makes it altogether probable that it can be used as a self-sown forage plant. This seems so obvious that it has been suggested that it might become a troublesome weed.

The development of this drought-resistant race of wheat has been deemed so important that an agricultural experiment station has been established at Haifa, with Aaronsohn as director, to develop this race along with drought-resistant races of other plants. It has long been known that the wild originals of barley, oats,

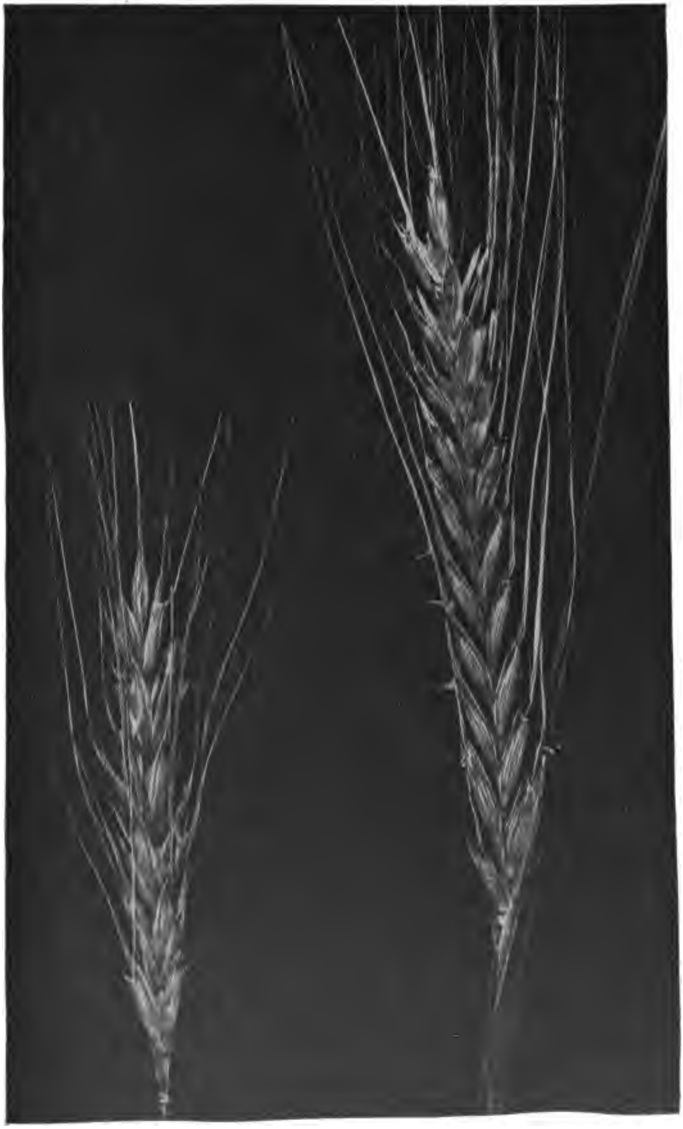

FIG. 67.—Heads of wild wheat grown at Bard, California, with anthers extruded and glumes spread.—After COOK.

and rye occur in Palestine; so that now Palestine may be regarded as "the cradle of the cereals." Aaronsohn has also entered into coöperation with the United States Department of Agriculture, so that plant-breeding experiments with this drought-resistant wheat are going on, not only in Palestine, but in various experiment stations throughout this country. It is too early yet to predict just when the results will be generally available, but there can be no question but that this discovery has made possible an important advance toward the solution of the food problem.

It should be realized why this wild resistant race is not simply pedigreed and multiplied in sufficient quantity for distribution. Although a vigorous plant with large kernels in its native habitat, it cannot be transplanted directly into a great variety of conditions and retain all its good qualities. Plants must be acclimatized; that is, they must become adjusted to new conditions. Races must be multiplied to meet all conditions of possible cultivation, either by selection or by crossing, or by both methods. The cultivated races of wheat have also become much diversified in the qualities of the grain, qualities that are adapted to various uses. The wild race, although vigorous in body and resistant to drought and disease, must be combined with qualities of grain that satisfy the present demands. The experiments at Haifa thus far have amply justified the expectations of Aaronsohn, for the wild wheat has proved to be very responsive to breeding experiments. Strains are being isolated, crosses are being made, and there is every reason to expect that this "new blood" injected into our races of wheat will revolutionize wheat production.

Another illustration of the possibilities of securing drought-resistant races may be obtained from the recent discovery of a drought-resistant race of maize. About the time Aaronsohn discovered wild wheat in Palestine, Mr. Farnham, a missionary in China, discovered a peculiar race of maize under cultivation by the Chinese. Since maize is known to be a native of the Mexican plateau region, Mr. Farnham was interested in tracing the time of its entrance into China. Upon consulting the Chinese records, he discovered that it had been under cultivation many years before the discovery of America by Columbus. This raises an interesting historical question as to the method by which the maize of Mexico reached China at that early date. It is obvious that a very small amount was brought, perhaps a single ear or two, because it proves to have been a case of unconscious pedigree culture. In this isolated region, therefore, this particular strain was pedigreed, and is now under somewhat extensive cultivation.

All those who are familiar with the cultivation of maize know that at a certain period in its development a "dry spell" is exceedingly dangerous. The reason for it is that the "silk," which is to receive the pollen, must be moist in order to be effective. If it is dried out or blasted, pollination will fail. If a drought comes, therefore, just when the silk is being exposed, complete pollination will not occur, and the crop will be more or less a failure. This new Chinese maize has such a structure that the silk is not exposed until after pollination. In fact, the silk elongates through a drift of pollen, so that when it is exposed it has already been pollinated. The leaves, instead of spreading widely as in the ordinary races of maize, are rather rigidly upright, so that a deep pocket is formed between the base of the leaf and the stem. When the pollen flies it collects in a drift in this pocket, at the bottom of which is the developing ear. More remarkable is the late and rapid elongation of the silk. Not until after the pollen has been scattered does the moist silk develop, of course growing through the drift of pollen. In this case, therefore, no dryness of the air can affect pollination. This race is under study, but has not been developed as far in breeding experiments as has the wheat.

It is rather remarkable that our two most important cereals, one being the basis of our bread supply and the other of our meat supply, should be the first to yield this result. If the maize should work out as the wheat has done, there will be no failure of maize crops on account of drought, and there will be maize fields as well as wheat fields throughout our semi-arid regions, provided there is moisture enough in the soil, which, of course, can be supplied by irrigation. The increase in annual food production when wheat and corn can be insured against drought and when the area of their cultivation can be doubled can hardly be calculated.

SUMMARY

The advance in plant-breeding has suggested the possibility of drought-resistant races of plants, thus not only insuring crops against drought, but also extending the area of cultivation of the fundamental crops into semi-arid regions.

The method suggested is first the discovery of drought-resistant races as wild plants in semi-arid regions, or as members of the mixed population usual in cultivated fields. When such races or strains have been discovered they must be bred for quality, either by continuous selection or by crossing with cultivated races of approved quality.

The discovery of the wild original of the wheat in Palestine has brought within the reach of plant-breeding a hardy, drought-resistant and disease-resistant race of vigorous body and large grain, which has just the qualities lacking in the ordinary cultivated races. An experimental station at Haifa, Palestine, in coöperation with the United States Department of Agriculture, is breeding this wild race for quality and for acclimatization, so that drought-resistant and disease-resistant races of approved qualities, and suited to the greatest variety of cultural conditions, may be obtained.

The discovery of a wild resistant race of maize in China has also made it possible to breed races of maize that will insure this important crop against drought, and will very much extend the area of its cultivation.

The work that has begun with these two most fundamental crops can be done for all crops, so that destruction by drought, and the unproductiveness of semi-arid regions should disappear.

CHAPTER XIII

PLANT DISEASES

In the cultivation of plants it is very important to learn to recognize and to control destructive diseases. So enormous have been the losses from plant diseases that a very conspicuous part of the work of the United States Department of Agriculture has been to investigate them, in the effort to discover their causes and to suggest remedies. Since this is also an essential part of the work of every State Experiment Station, the literature dealing with plant pathology has become very extensive. There are at present certain limitations of plant pathology, however, which should be understood.

The general definition of a plant disease should include any interference with the normal activities of a plant, but this would include a far greater variety of causes than are considered as yet in plant pathology. Such a definition would include parasitic fungi, animal attacks (especially insects), mechanical injuries, unfavorable climatic conditions, unfavorable soil conditions; in fact, anything that affects unfavorably the tone and vigor of the plant. In practice plant pathology has been restricted almost entirely to a study of diseases induced by parasitic fungi, but its future development will include a wider range of diseases.

Still another restriction is inevitable. All plants have their diseases, but our economic interests have compelled attention chiefly to those diseases that attack cultivated plants; just as animal pathology is concerned chiefly with the diseases of domesticated animals and man. The problem of diseased conditions in plants in general is one of great scientific interest, but the diseases of cultivated plants have as yet furnished such important practical problems that the wider field has not been cultivated. In practice, therefore, plant pathology is in general restricted to the study of the diseases of cultivated plants induced by parasitic fungi.

It is very common to confuse the disease with its cause, and this has led, not only to much misunderstanding, but has also diverted plant pathology from its real subject. It is important that a disease and its cause be kept distinct. For example, a very common disease of wheat is called "wheat rust," but the rust is an attacking fungus which causes a disease; it is the wheat plant which has the disease. The bulk of pathological literature dealing with plant diseases is an account of the life histories of the parasites that cause disease. This is very essential, but it is merely preliminary to a study of the disease itself, a fact which has long been recognized in the study of human diseases.

The disease is the unfavorable reaction of the attacked plant (host) to the presence of the parasite. This reaction is a physiological one, which may or may not express itself in abnormal structures. Plant pathologists are recognizing this, and have begun to study these physiological reactions which represent the pathological condition of the host. In other words, plant pathologists are beginning to study the "patient" as well as the causal organism. It would seem like strange human pathology to study only the bacillus of typhoid fever, and not to study the pathological condition of the typhoid patient. The study of abnormal physiology requires a knowledge of normal physiology, and this has only recently reached such a stage among plants as to make the study of abnormal physiology effective.

At present we know comparatively little of the pathological responses of the host plant to an attacking parasite. The most we have done is to note whether the pathological condition expresses itself in abnormal structures or behavior. We note the cause and the result, but how the cause produces the result is the important problem. It is clear that all plant therapeutics will remain empirical until we know something of the physiological reactions that occur between the cause and the result.

It is the usual custom to give an account of plant diseases by presenting a list of the fungi that induce them. In other words, such an account gives no classification of diseases, but simply of disease-producing fungi. As a matter of fact, similar diseases are induced by a great variety of fungi, diseases presenting the same symptoms and the same results. An occasional custom is to give an account of plant diseases by presenting a list of the plants attacked (hosts). This has the advantage of making a disease more easily recognized, for most persons know the patient, while it requires expert knowledge to recognize the attacking parasite. However, many plants have similar diseases, and in such an account the same symptoms are given with monotonous repetition. The real basis of presentation is a classification of the diseases themselves, based upon the nature of the disease, induced by whatever groups of fungi, and occurring on whatever hosts. Such a classification may be made, based upon the relations of parasite and host, and it results in placing most diseases in three categories, each category having its recognizable symptoms. Before describing these categories, however, a brief account of the parasites inducing diseases will be helpful.

Conspicuous among disease-producing organisms are bacteria. They are the most minute, and therefore the most subtle, of parasites in their attacks. They may reach their hosts in a great variety of ways, such as lodging in wounds, carried by insects, spread by rain, entering from the soil, etc. In perennial hosts in many cases the disease-producing bacteria live from year to year, being what are called *perennating* forms. Bacterial diseases are the most difficult to determine, simply because the causal organism is so illusive. It has often taken many years to determine that a given disease is bacterial in origin, as in the case of pear blight and crown gall. It should be realized that bacteria as a rule cannot be identified by sight, but they must be recognized by their behavior; hence it is not merely a question of examining them under the microscope, but of "cultures," and these cultures tell of their appearance and behavior in masses.

If a parasitic organism has been isolated in cultures from a diseased plant, and suspected of being the cause of the disease, this suspicion must be tested. This is done by inoculating healthy plants with the cultures, and if the disease appears as a result the causal organism has been demonstrated. Often causal organisms that appear alike and behave alike in cultures prove to be unlike in their relations to hosts. For example, the causal organisms inducing "wilt" of cotton, cowpea, and watermelon, when isolated in cultures, seem to be exactly the same organism in all three cases, but when "cross inoculations" were tried, as, for example, inoculation of watermelon with the organism obtained from diseased cotton plants, the disease did not develop in the watermelon, and so for all the cross inoculations.

This means that very often differences between attacking parasites cannot be detected except by the fact that they attack different hosts. In other words, there is some specific relation between host and parasite. Such species of parasites are called "physiological species" in contrast with "morphological species," which can be distinguished by their appearance. When a causal organism is isolated and tested, therefore, it is very customary to try inoculation of related hosts to discover how far the parasite is restricted in its attacks.

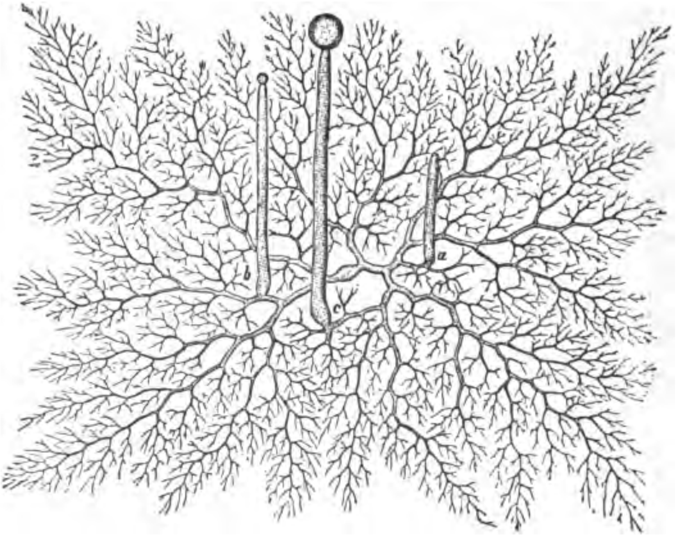

FIG. 68.—Diagram of a mold (*Mucor*), showing the profusely branching mycelium and three spore-bearing branches.—After ZOPF.

The "true fungi," as distinct from bacteria, include the great majority of the parasites inducing diseases among cultivated plants. A true fungus is recognized by the fact that its body consists of filaments, which may be interwoven more or less compactly. For example, the weaving may be so loose that the body is as delicate as a spider web, or it may be so close that the

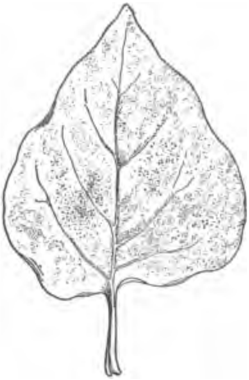

FIG. 69.—Lilac leaf covered with mildew.

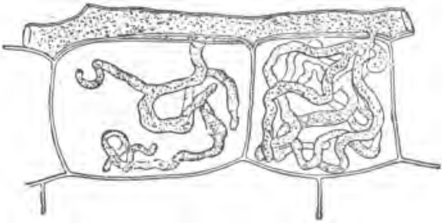

FIG. 70.—Downy mildew: branch of mycelium in contact with two cells of a host plant, into which sucking branches (haustoria) have penetrated.—After DEBARY.

body becomes very compact. This filamentous body is called a *mycelium* (Fig. 68). The mycelium must be related to its food supply, and therefore the mycelium of a parasite either spreads over the surface of its host, or burrows among the tissues within the body of the host; that is, there are external and internal parasites.

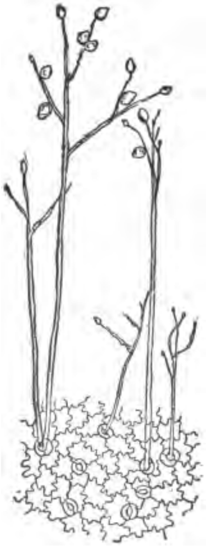

FIG. 71.—Spore-bearing branches of downy mildew emerging through the stomata ("breathing pores") of a leaf.—After STRASBURGER.

For example, when a "powdery mildew" attacks a lilac bush its mycelium spreads over the surface of the leaves (Fig. 69); but when a "downy mildew" attacks a grape vine it burrows among the working cells in the interior of the leaves (Fig. 70). The mycelium also sends out sucking appendages that penetrate the cells of the host and absorb the nutrition (Fig. 70); and it also sends up branches that bear spores which produce mycelia on other plants (Figs. 71 and 72). In the case of internal parasites the spore-bearing branches must reach the surface of the host, so that the spores may be in a position to be scattered (Fig. 71). Often the only superficial indication of an internal parasite is a coming to the surface of the spore-bearing branches. For example, the wheat rust which appears on the stems and leaves of the wheat plant as reddish dots and streaks, is the mass of spores sent to the surface from the deep-seated and wide-ranging mycelium (Fig. 73).

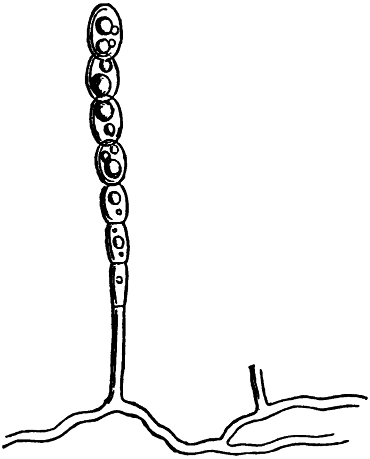

FIG. 72.—Spore-bearing branch of a superficial mildew with its row of spores.—After TULASNE.

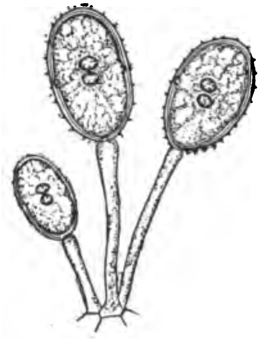

FIG. 73.—Summer spores (uredospores) of wheat rust.

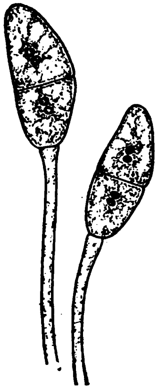

FIG. 74.—Winter spores (teleutospores) of wheat rust.

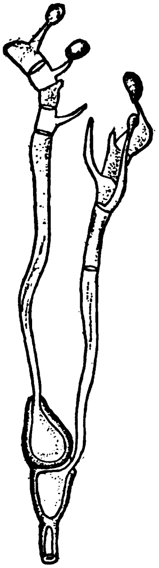

FIG. 75.—A winter spore of wheat rust germinating and producing two small mycelia with spores.—After TULASNE.

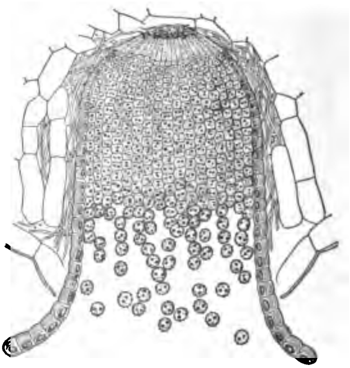

FIG. 76.—The cluster-cup (on barberry) of wheat rust, containing rows of spring spores.

Another feature of many true fungi that often makes their study extremely difficult is the fact that they pass through several phases during their life history. For example, the mycelium of the wheat rust lives on wheat plants and produces two kinds of spores. One of these kinds produces mycelia on other wheat plants, and thus spreads the disease (Fig. 73). The other kind of spore, which appears late in the season (Fig. 74), lasts through

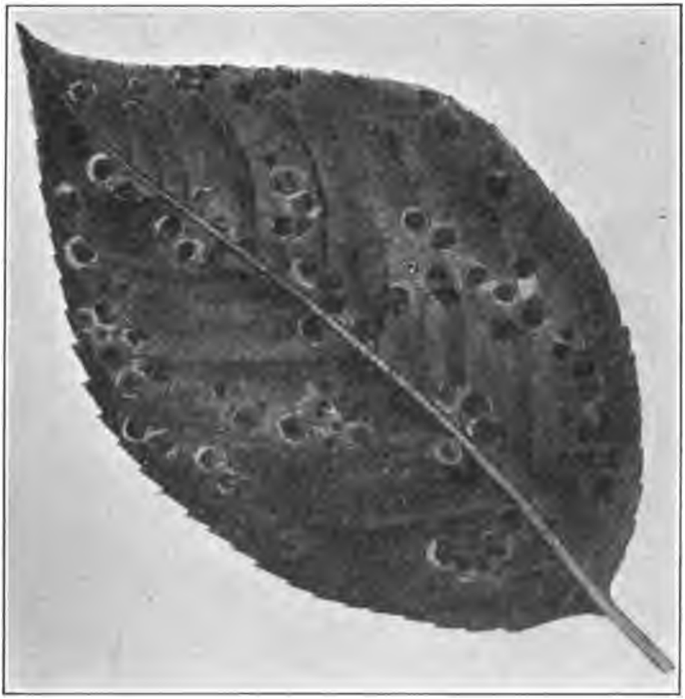

FIG. 77.—A spot disease of apple leaf.—After SORAUERER.

the winter, and in the early spring produces a small mycelium which is not a parasite, but produces spores (Fig. 75). These spores reach the young leaves of some host other than wheat, as, for example, the barberry, and develop a mycelium on the barberry leaves (Fig. 76). This mycelium produces spores, and these spores infect the wheat plant. In this life history, therefore, two different kinds of hosts are involved and several kinds of spores. In very many cases the mycelium and its spores on a given host are well known, but to what mycelium upon some other host they may be related in a life cycle is unknown.

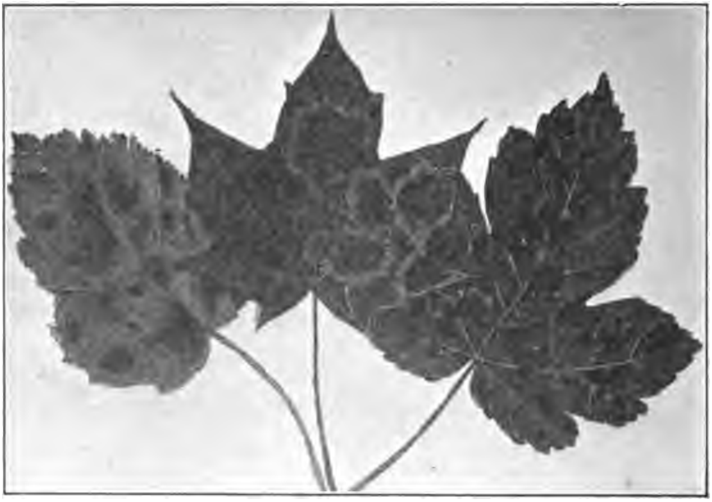

FIG. 78.—A spot disease of maple leaf.—After SORAUBER.

As stated above, plant diseases may be referred to three categories, based upon the relations of parasite and host, and each category has its own symptoms. These categories may be indicated as follows:

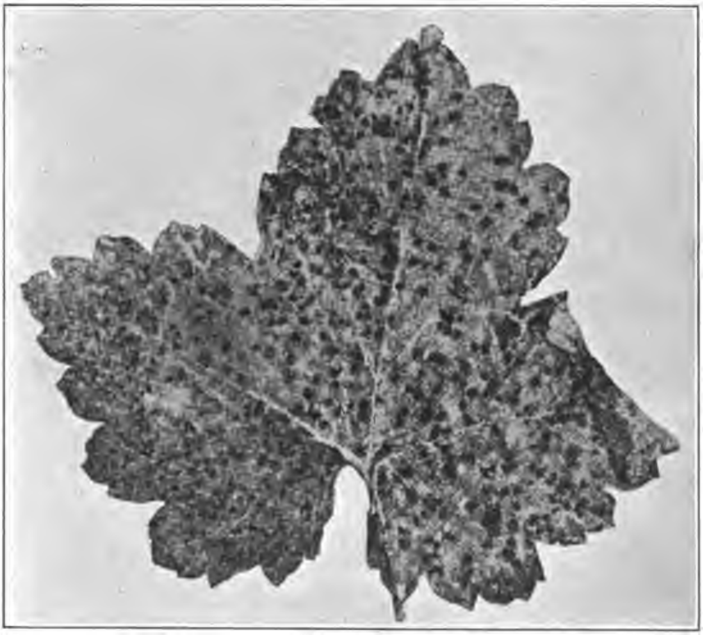

FIG. 79.—A spot disease of currant leaf.—After HALL.

(1) *Parasites immediately destructive.*—The structure destroyed by such parasites is the living protoplast, and therefore there may be destruction of protoplasts that does not result in the destruction of the host as an individual. The destruction of the host de-

pends upon the number and kind of protoplasts destroyed. For example, when a parasite attacks a leaf and destroys a few protoplasts here and there, resulting in a "spotted" leaf, the plant as a whole survives

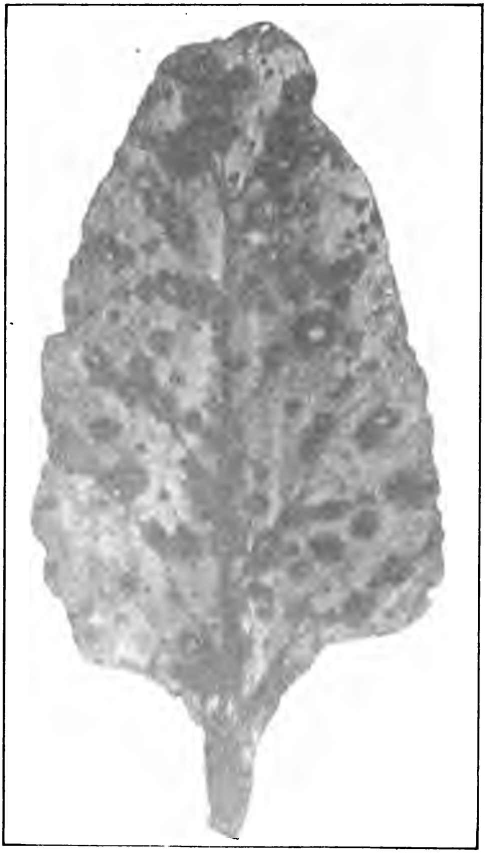

FIG. 80.—A spot disease of beet leaf.—After HALSTED.

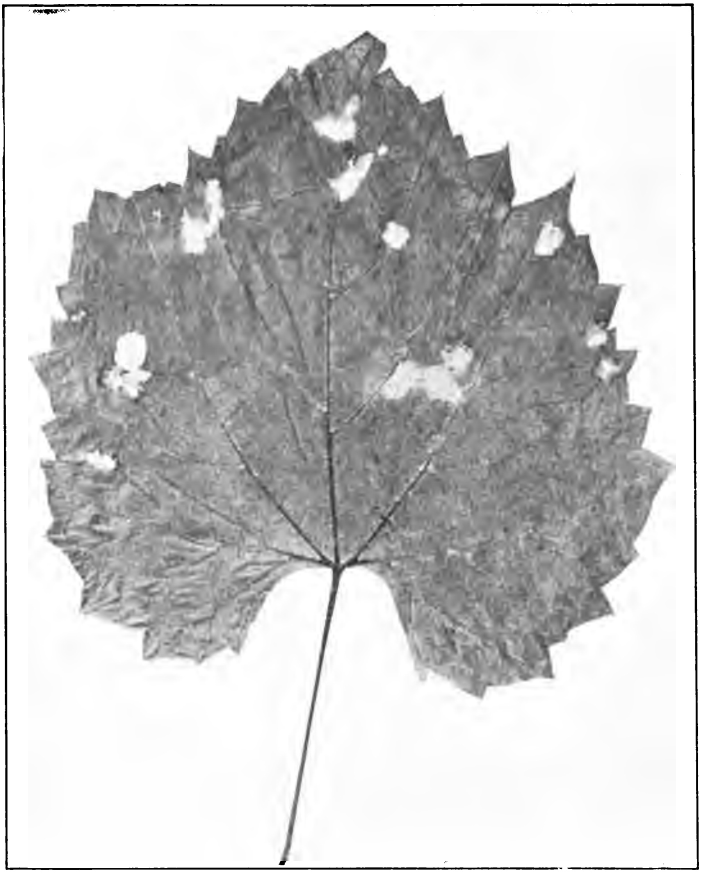

FIG. 81.—Grape leaf showing patches of downy mildew.

(Figs. 77-80). But if there is a more extensive destruction of protoplasts, so that the activities of the plant are interfered with seriously, it may be weakened at first, and finally killed. The economic loss does not depend upon the fact whether the host plant is killed or not, but upon the effect of the parasite upon the part of the plant that is used. For example, grape mildew may not affect grape vines seriously, but in addition to spotting the leaves (Fig. 81), it spots the young grapes, and this results in an economic loss.

The protoplasts are killed as soon as the cells are invaded, or they may be killed before invasion by the action of excreted enzymes. The parasite kills the cells, and then lives on the soluble food substances that diffuse through the dead and dying protoplasts. Such parasites, therefore, live as saprophytes; that is, they do not feed upon living material, but upon material that has been killed, or that is no longer connected with the life processes. This means that such parasites can be cultivated artificially; that is, apart from the host, all that is necessary being to supply nutritive solutions. When cultures of a true fungus parasite are possible, therefore, it belongs to this category.

Furthermore, since the invaded cells are killed, the host cannot react by abnormal growth, resulting in what is called a *hypertrophy*. There may be a growth reaction such as follows any wound, a reaction that heals the wound and usually leaves a scar; but this wound reaction is not a specific reaction of the host to the parasite; it is simply a reaction that follows any wound.

(2) *Parasites not immediately destructive.*—This means that the parasite and the protoplast live together in intimate association for a time, without any apparent injurious effect, certainly without fatal effect, on the host cells. This living together of two organisms is called *symbiosis,* and this relationship of parasite to protoplast is therefore a symbiotic relationship. The period of this peaceful symbiosis is brought to an end when the fungus begins to form spores. Probably the real fact is that the protoplast is gradually weakening, and that when it is approaching destruction spore-formation occurs.

It follows that such parasites cannot be cultivated artificially; that is, apart from the host. They are real *obligate* parasites, of which rusts and smuts are conspicuous examples. No one has been able to produce artificial cultures of the spores of rusts or smuts beyond the very earliest stages of germination. The reason for this necessary association of host and parasite is probably due to the fact that the parasite is dependent upon what are called the intermediate products of metabolism; that is, products that appear in life processes of the protoplasts, but which do not occur outside of living cells. In other words, we cannot reproduce them in artificial nutrient solutions, and therefore such parasites cannot be cultivated artificially.

Since the host cells are not killed, but remain active through a long period, they are capable of growth, and the presence of the parasite frequently results in what is called a growth stimulus, to which the host plant responds in a variety of ways. Sometimes there is no apparent response in growth, as in many rusts, smuts, and mildews. In other cases there is simply a great enlargement of the affected cells, resulting in growths that resemble little blisters. The conspicuous responses

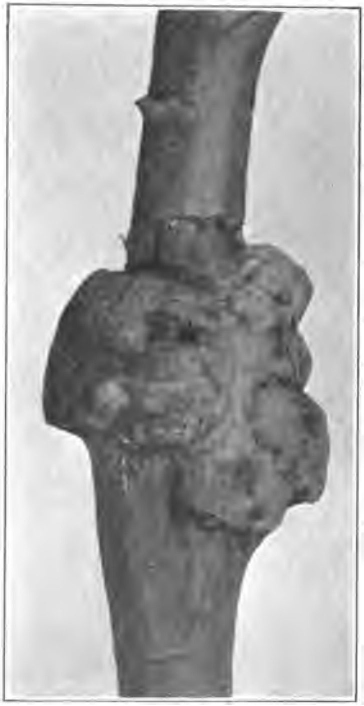

FIG. 82.—Crown gall on daisy.—After ERWIN SMITH.

to the growth stimulus, however, are cases in which it results in distinct hypertrophies, which are abnormal growths, such as galls (Fig. 82), cedar apples (Fig. 83), witches' brooms, etc. Nothing is known as to the cause of this growth response further than that it is due to the presence of the mycelium. Therefore, accounts are limited to descriptions of the forms of the hypertrophies and of the tissue elements that enter into

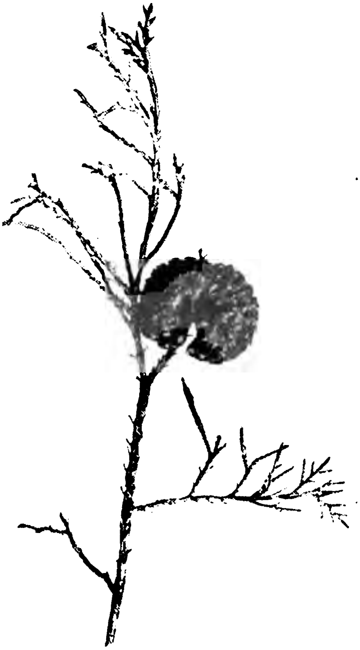

FIG. 83.—A cedar apple.

them. This is another case in which the cause and the effect are known; that is, the parasite on the one hand, and the hypertrophy on the other, but there is no knowledge of the factors and the processes that lie between.

(3) *Xylem invasion.*—The parasites that invade the wood tissue (xylem) are not true parasites, as they do not attack living cells, either by destroying protoplasts or by living in symbiotic relations with them. They simply find in the water (sap) being conducted by the xylem a suitable nutrient solution. It follows that they are not dependent upon the host, but they find in the host a most available source of food supply. Evidently such parasites, not being destructive of living cells, are not immediately destructive of the host, but there is eventually a wholesale destruction of the host by cutting off its water supply. It is as though the water-pipe system of a house had become choked up. The very numerous so-called "wilt diseases" among plants are largely due to this kind of relation between the so-called parasite and the host. The disease in this case is hardly a pathological response on the part of the host. It is really a disease in the sense that drowning or hanging are diseases.

The three categories of plant diseases have been put together compactly in order that they might be contrasted sharply. These categories will become more concrete by giving a few illustrations under each one.

Among the common diseases that are induced by parasites which are immediately destructive is the pear blight, a bacterial disease. In this case the nectaries of the flowers are infected by visiting insects. The bacteria spread from the nectaries to all living tissue. The protoplasts are destroyed and the branch tips begin to wilt, and then blacken. As a result of this

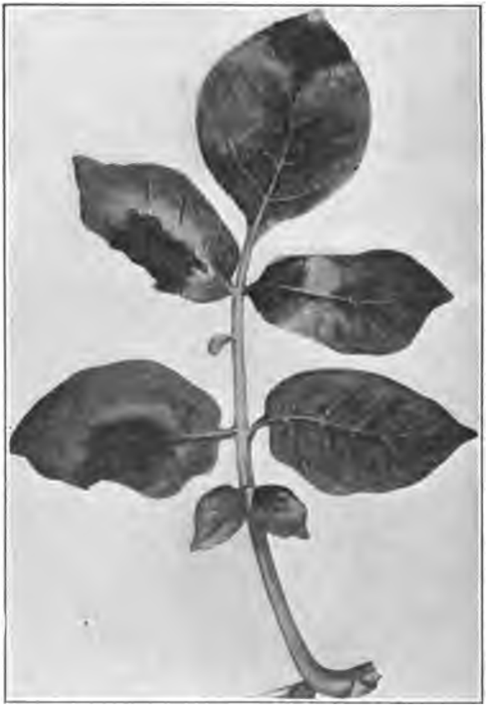

FIG. 84.—Potato disease on the leaves.—After JONES.

appearance of the infected branch the disease is often called "fire blight," meaning that the branch tips appear as though scorched.

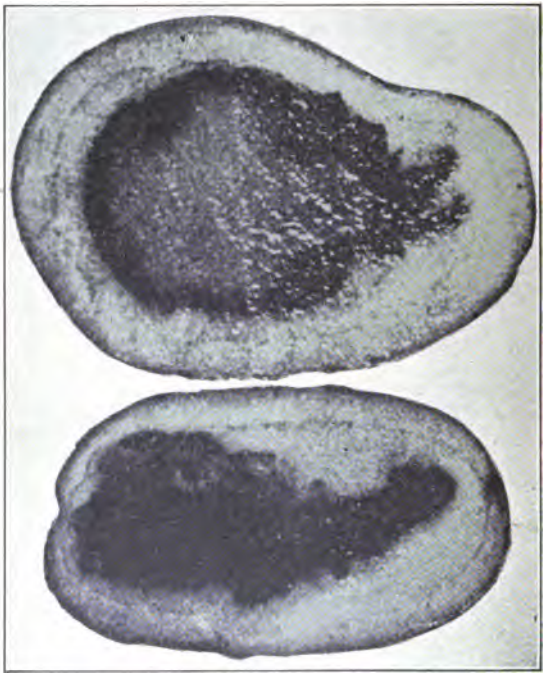

FIG. 85.—Potato disease ("potato rot") in tubers.—After DUGGAR.

The various leaf-spot diseases (Figs. 77-80) are also illustrations of such parasites, the protoplasts of the leaves being killed in groups, resulting in brown or black spots. As these spots multiply, naturally the important work of the leaf is interfered with, so that the plant becomes a less efficient machine.

Among other diseases of the same sort may be mentioned the potato rot (Figs. 84 and 85); the bitter rot of apples (Fig. 86), which is a fruit attack; the powdery mildew of the grape; cankers of various kinds, which are open wounds found in tree plantations and orchards (Fig. 87).

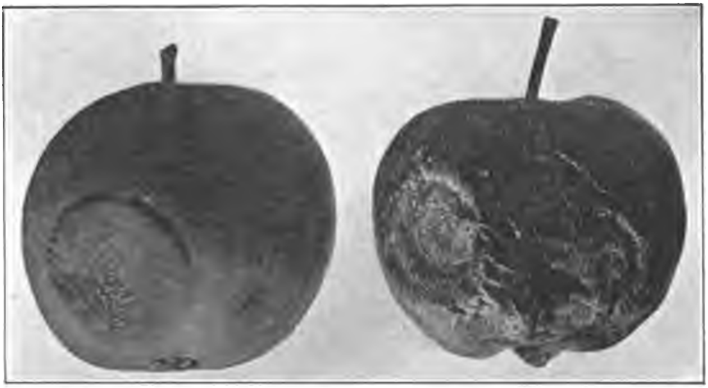

FIG. 86.—Bitter rot of apple.—After CLINTON.

In all such cases the universal symptom is more or less killed tissue, giving a blasted or spotted appearance, and, of course, the entire absence of any hypertrophies. Such diseases are induced by a great variety of parasites upon a vast number of hosts, but the symptoms and the practical treatments are the same.

Among those parasites that live symbiotically with the host protoplasts are those that induce such diseases as peach-leaf curl; black knot of plum and cherry (Fig. 88); crown gall (Fig. 82); and various root diseases resulting in distorted roots. The crown gall is a very interesting disease which has recently been studied. The hypertrophy is a large tumor-like swelling frequent on trees, which occurs just where stem and root join. This abnormal growth is found to be due to the presence of bacteria, and the spread of the trouble through the tree shows certain resemblances to the behavior of human cancer, for which as yet no causal organism has been found.

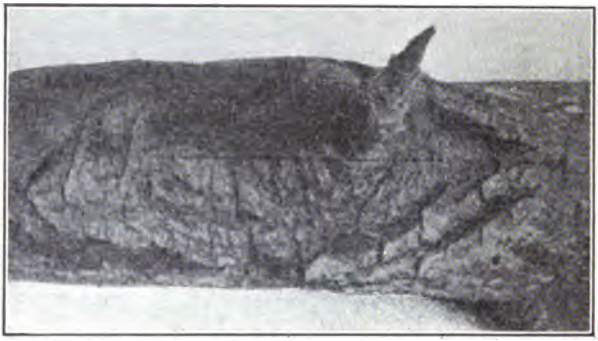

FIG. 87.—Canker of bitter rot on apple twigs.—After BURRILL.

There are some very interesting facts connected with hypertrophies that may be mentioned. In the first place, when a hypertrophy develops, a certain tissue responds to a given parasite. In other words, there is some specific relation between the parasite and the tissue. In the second place, the tissues produced by the hypertrophy are just such as the specific tissue is in the habit of making, but of course they are produced excessively. It follows that when the cambium of a tree is the specific tissue responding to the growth stimulus of a parasite the hypertrophy, as the crown gall or the cedar apple, is very complex anatomically, since the cambium makes more kinds of tissue than any other growing cells. In the third place, it is evident that the uninvaded cells are the ones that respond, for they are the only ones in a condition to respond to the growth

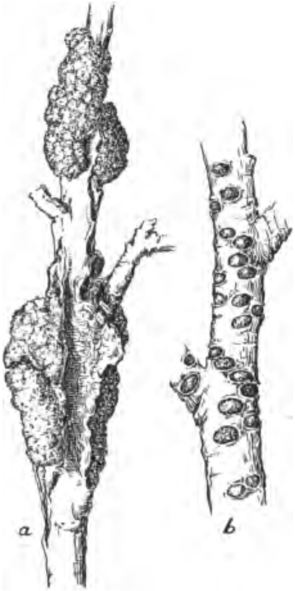

FIG. 88.—**Black knot:** *a*, **on plum;** *b*, **on currant.—After MASSEE.**

stimulus. Therefore, whatever this stimulus may be, it is transmitted from the infected cells to those that respond.

Illustrations of the diseases resulting from xylem in-

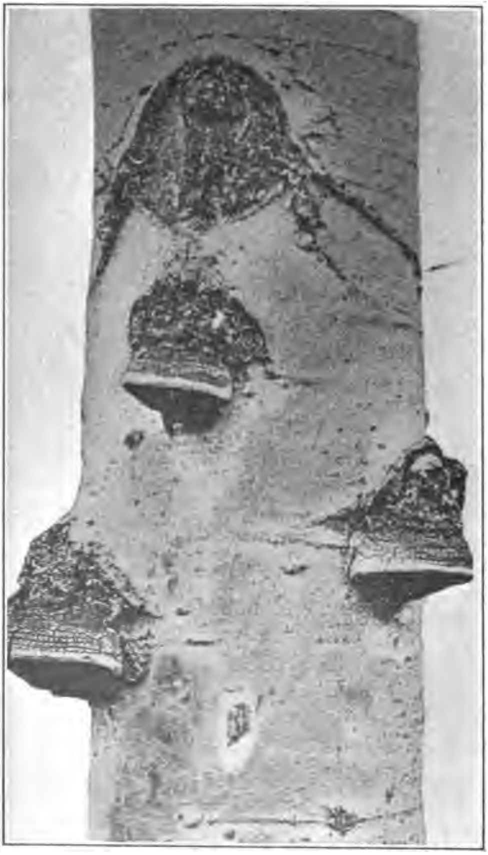

FIG. 89.—Tree fungus on aspen.—After VON SCHRENK and SPAULDING.

vasion are the numerous "wilts" already mentioned. The best studied of the wilts are those of the cotton, cowpea, and watermelon, which are of very great economic importance throughout the southern states. Notable illustrations are the wilts that occur in many forest trees, resulting from the mycelium of mushrooms, whose spore-bearing branches appear on the trunks of trees as brackets (Figs. 89 and 90), toadstool forms, etc. These are great timber destroyers.

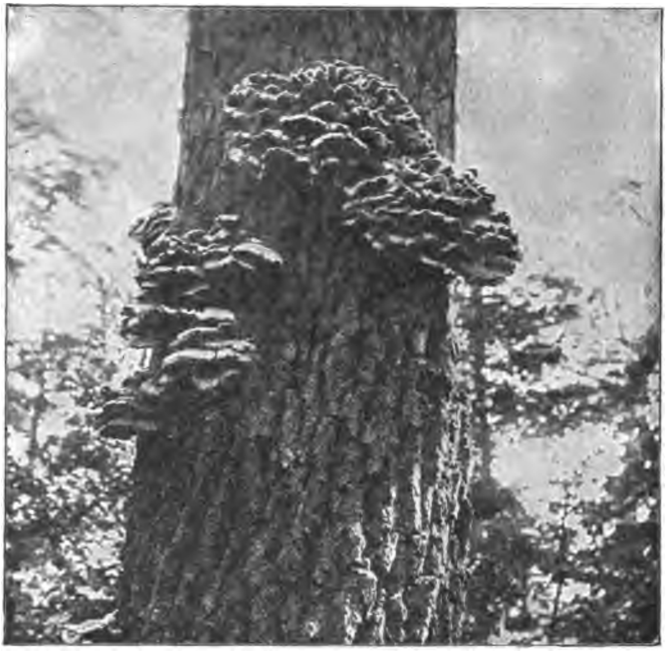

FIG. 90.—A bracket fungus growing on a red oak.

This statement needs explanation, for diseases resulting from xylem invasion have been defined as those in which the parasite does not invade living cells, either to destroy the protoplasts or to live symbiotically with them, but simply plugs up the xylem and chokes the "water pipes." The xylem (wood), however, is composed of dead cells which are conducting water, and the mass of xylem constitutes the timber. Interfering with the water supply, and thus weakening or killing the tree, would not injure the timber, but in the life processes of the fungi living in the water, stream substances are given off (excreted) which "corrode" the walls of the xylem cells in such a way that the wood becomes brittle or corky and entirely unfit for lumber.

Until recently the treatment of plant diseases consisted chiefly in trying to control them by means of fungicides. When the sources of infection were discovered, and were found to be reached by fungicides, control became very complete in many cases. Further statement in reference to the use of fungicides will be made in the next chapter.

Another method of treating plant diseases is by plant surgery, which means the removal of infection. Like all surgery, this has to guard against further infection, and much of it is done thoughtlessly or needlessly. It is particularly used in connection with shade trees. In tree surgery one must be sure of three things: (1) whether an infection exists in the part proposed to be removed; (2) if so, whether it will do any good to remove it; and (3) if so, whether it can be removed. Much surgery is undertaken without any recognition of these conditions. Two illustrations will help to make the situation clear. In pear blight the destructive bacteria winter in the twigs, which gradually blacken as if scorched. In this case the infected part is obvious and it can be removed successfully. In crown gall (Fig. 82) an unsightly tumor-like growth develops near the base of a tree, but from it there extend into other regions "infecting strands" that result in new galls, thus spreading the trouble. In this case the infection (bacteria) exists in the gall; the gall can be removed; but it will do no good to remove it on account of the infecting strands which cannot be removed. Of course, "tree surgeons" operate upon crown galls that are common upon street trees, but they have no conception of the real situation. The simplest and most effective surgery is in caring for the wounds of trees that arise from broken branches or from pruning. It consists simply in securing a fresh surface for the wound, thus permitting the development of wound cork, and then covering the surface with something that is impervious to wound-invading fungi.

The final resort in the control of disease is the cultivation of resistant races. When nothing else avails, resistant races must be resorted to. This will probably be finally the ultimate remedy for all plant diseases;

but those that can be controlled can afford to wait. Work upon resistant races, therefore, as yet has dealt chiefly with diseases that arise from soil infections. This important subject of the cultivation of disease-resistant races will be discussed in the next chapter.

SUMMARY

Plant diseases as ordinarily studied are due to an invasion of parasitic fungi, either bacteria or the true filamentous fungi. The invaded plant (host) reacts to the presence of the parasite, and this reaction, when it is unfavorable to the host, constitutes the disease.

Plant diseases may be referred to three categories, dependent upon the relation between parasite and host, each category having its own symptoms by which it may be recognized.

One category includes those diseases in which the parasite immediately destroys a protoplast and lives upon its dead or dying body. The destructiveness of such a parasite depends upon the number and nature of the protoplasts destroyed. Such diseases may be recognized by killed tissue (spotted leaves, blighted twigs, etc.); by the fact that the causal organism can be cultivated artificially; and also by the fact that no hypertrophies (abnormal growths) are produced.

A second category includes those diseases in which the parasite enters into symbiotic relations with the protoplast, not destroying it, but living upon its products. Such diseases may be recognized by the absence of killed tissue; by the fact that the causal organism cannot be cultivated artificially; and chiefly by the fact that hypertrophies usually appear in the form of contorted growths and galls of various kinds.

The third category includes those diseases in which the parasite does not invade living cells, but invades the xylem (the water conducting system) and cuts off the water supply, resulting in wilting.

In controlling these diseases exact knowledge of the sources of the infection is absolutely necessary. Infection may come from transported spores, soil infections, wound infections, perennating mycelia, etc. Superficial infections, as lodged spores, may be treated with fungicides, but soil infections and mycelial invasion cannot be controlled in this way.

The most difficult diseases to control are those arising from soil infections. The only known method is to stop planting the infected area with the susceptible crop and plant some other crop until the infecting organism has disappeared or has become relatively inactive.

The final resort in the control of diseases is to secure disease-resistant races of plants, which has been done in several cases of soil infections.

CHAPTER XIV

HOW TO SECURE DISEASE-RESISTANCE

That plants, as well as animals, are subject to destructive diseases was made evident in the preceding chapter. The annual destruction of crops from this cause is enormous. The work of the United States Department of Agriculture in maintaining a group of experts to investigate the causes of various diseases and to develop remedies has been mentioned. The results have been very important. The parasites inducing many diseases have been discovered, their life histories have been studied, and methods of control have been devised.

The advance in the method of combating plant diseases has run parallel with that of combating human diseases. The first search was for remedies to check or cure the disease after it had appeared, a method which must always be in vogue. The advance consists in the attempt to prevent disease, the idea being the same as that underlying what is called "preventive medicine." It so happens that this can be carried further with plants than with human beings, for diseased plants can be destroyed, while diseased human beings must be saved if possible. It is evident, therefore, that such susceptibility to plant diseases as is inheritable comes within the scope of plant-breeding to eliminate; and that if immunity to disease is inheritable, plant-breeding can substitute immune races for susceptible ones. Among human beings the susceptible ones must not be destroyed, although they generally disappeared until the recent wonderful advance of medicine. As a consequence of this advance, the human situation has become much more complex and difficult, for susceptible individuals are kept alive and associate with immune individuals. In dealing with plants, however, there is no reason for saving susceptible individuals if immune ones can be substituted for them.

It will be well to understand something of the treatment of plant diseases, so that the place of plant-breeding may be evident. Before there was any scientific study of plant diseases, experience, under the pressure of necessity, had developed many treatments. Some of these empirical treatments have been proved to have a scientific basis, while some of them have been proved to be little more than superstitions. An interesting illustration of the chance discovery of a valuable fungicide is that of the Bordeaux mixture, probably the most used and most useful of all the fungicides. When the American grape vines were introduced into Europe in the hope of getting rid of the destructive phylloxera by grafting the wine grape upon the resistant native grape stock of America, the result was the introduction of a still more destructive disease, the grape mildew. In consequence, for several years the grape crops of France and Italy were failures, and every method of treatment was tried. In southern France it had long been the habit to sprinkle several rows of vines next to the highways with a copper sulphate mixture, so as to give to those passing the impression that the grapes were poisoned. During the ravages of the grape mildew it was discovered that the vines in these treated rows were free from the disease. As a result of this observation Bordeaux mixture, a mixture of copper sulphate and lime, was developed, and proved to be a specific in controlling the disease.

There is no intelligent control of disease possible until there is exact knowledge of the sources of infection. These sources are extremely various. For example, the infection may be due to spores, and the spore-carriers are wind, insects, raindrops, seeds, or a number of other agencies; and the spores in turn affect various organs as well as organs of various ages. Then there are wound-infections, the parasite entering through wounds made in a great variety of ways, either naturally or artificially. There are also infections arising from parasites, especially bacteria, that continue to live season after season in the perennial host. Finally, there are soil-infections, which are peculiarly baffling.

The most common method of controlling a plant disease is to apply a fungicide in such a way as to prevent infection. It is obvious that this is effective only in cases where spores lodge for germination or where the parasite is an external one, and that it is of no effect if the infection is from the soil or from a parasite living from season to season within the host. When it is discovered that a fungicide is appropriate, the next thing is to know when to apply it. For example, if infection is from spores lodging upon bud scales in a position to attack the unfolding leaves, the fungicide must be applied to the buds before they open. If infections are produced by successive crops of spores during the season, the fungicide must be applied at intervals throughout the season. Each case has its own period or periods of treatment.

In cases of soil-infection it is now found that fungicides are not available. This will become obvious when the necessary life of the soil is remembered. It is now well known that the soil is teeming with a population of organisms that are necessary to keep it in condition for plants. Any fungicide applied to the soil is in danger of destroying this population. The application of a fungicide to the soil, therefore, in order to kill a specific parasite that is harboring in the soil, would be much like annihilating the whole population of a city in order to destroy a single criminal. The only known method of control in the case of soil infection is to stop planting the susceptible crop upon the infected area, and to plant some other crop. This rotation has been found to be beneficial in eliminating or weakening infection. Just how this is accomplished is not clear, but the results are apparent. In the case of wilt diseases that attack cotton, cowpea, and watermelon, for example, all of which involve soil infections, definite rotations have been worked out that hold the trouble in check. The period during which a susceptible crop should not be planted in an infected soil varies, of course, with the causal organism. Some of these organisms seem to be able to persist indefinitely, even in the absence of a susceptible host; in which case any practicable rotation must involve some injury to the organism by the cultivation of immune crops. In any event, although infected soil cannot always be disinfected by rotation, the disease can be materially checked.

The above very brief statement in reference to the control of plant diseases indicates that it is a very laborious and often more or less doubtful process. There are certain simple infections for which appropriate fungicides are easily applied and are specifics, but in far the larger number of cases the treatment is indefinite except in the hands of a specialist. It is clear that the final resort in reference to plant diseases will be the breeding of resistant races, and it is becoming obvious that this is possible with all cultivated plants. Work upon resistant races thus far has been restricted largely to diseases that arise from soil infections, for diseases that can be controlled by fungicides can afford to wait.

The whole subject of immunity is a very interesting one, and its cause is yet largely a matter of theory. It is well known that certain varieties of plants are less subject to attack by certain diseases than their relatives. In fact, relatively resistant varieties are well known among all our crop plants. It is clear, however, that predisposition to attack does not necessarily depend upon an enfeebled condition of the plant, for plants in as good normal health as their resistant relatives are attacked. It is also true that susceptible plants are often subject to attack only during certain stages of their development. Young parts are especially subject to attack, and later may become completely resistant. In none of these cases does infection depend upon any injury to the health of the plant, although this is a very common opinion. And yet there is evidence that immunity may hold some relation to vigor. For example, certain disease-resistant races of cotton, referred to later, proved to be less resistant when transferred to other regions; and also less resistant in certain seasons. The only difference observable in both of these cases was a lack of vigor in the plants. The new areas were not favorable for vigorous growth, and certain seasons were ''poorer seasons'' than others. Moreover, in the development of disease-resistant races of potato it has been found that immunity may gradually disappear in succeeding generations.

In view of such facts, if one considers the numerous differences among plants that would affect the entrance and food of parasites, the list would be something as follows:

Plants differ widely as to the ease with which their superficial structures can be penetrated by a fungus. A relatively impenetrable tissue, therefore, might often make a plant resistant to a certain disease, and there is no more common difference among plants than a difference in superficial tissue.

Plants also differ widely as to the substances they produce in their metabolism. In this case it is evident that certain plants may not produce the specific substances that a given parasite needs. This is borne out by the well-known fact that different parasites are usually restricted to particular plants. For example, certain fungi are restricted to members of the mustard family, and apparently this can be explained only by the fact that in the metabolism of this family the appropriate food substances are produced, substances not produced by other families. More frequently, a particular parasite is restricted to a single kind of plant, and parasites have distinguished varieties of plants before botanists have recognized any distinction. This must mean that the products of the metabolism of plants are extremely variable. It is also true that among the substances produced by plants there may be those which are specific poisons for a given fungus, and in this way resistance to this fungus would be secured. There are also a few cases known in which the invading fungus is overstimulated by some substance produced by the host, and destroys protoplasts with which it should enter into symbiosis, thus destroying its food supply.

In considering these various situations, it is evident that immunity may be due to a variety of factors or combinations of factors. A fungus may not be able to enter the host on account of impervious superficial structures; it may be able to enter the host, but may not find its appropriate food; its appropriate food may be present, but there may also be a toxin that destroys the fungus; or some substance may stimulate the fungus into such activity that it destroys its source of food. It is also obvious that these conditions of structure and metabolism may vary, not only in different plants, but also in different ages of the same plant, and in different organs of a plant. It would follow also that a plant ordinarily resistant to a disease might not remain so if any conditions of growth were unfavorable to the development of resistant structures or products. In other words, there is opportunity here for the greatest variation of plants in immunity, and also for variations in the same kind of plant growing in different localities and in different seasons.

In summarizing the above statements, it is apparent that resistance involves the structure and the metabolism of the host plant, just such features as may be expected to be inherited, for they constitute the essential differences among plants. It follows, therefore, that plant-breeding can be turned to account in selecting and developing races of plants resistant to the various destructive diseases.

The selection of disease-resistant strains is not so difficult as it might seem to be at first. For example, when an unusually destructive disease was ravaging the cotton fields of the Southern States, the Department of Agriculture sent some of its pathologists to investigate. In the ravaged fields they discovered certain plants that were as vigorous as if no disease had been raging. In other words, they were for some reason immune to this disease. Such a fact is familiar to human experience. In previous times, when plagues occurred, they never destroyed a whole population, but there were always left a large number of immune individuals. If this were not true, the human race would have been destroyed long before this. One of the reasons why the Chinese race is so resistant to many diseases is that through thousands of years there has been going on an unconscious pedigree culture for immunity. The condition of medicine was such that susceptible individuals disappeared, and as a result there has developed a remarkably resistant race. In the case of the ravaged cotton fields the immune individuals suggested the idea of pedigreeing them to discover whether this immunity is inheritable. This proved to be the case, and so resistant races of cotton have been developed.

This finding of immune individuals and pedigreeing them is possible whenever a disease is ravaging a crop. In the case of the wild wheat of Palestine, already referred to as drought-resistant, it was discovered that it was also resistant to wheat rust. Long cultivation of the wheat, therefore, has resulted in so changing its tissues or metabolism or both, that it has lost its resistance to rust. This suggests that a race of plants immune in one locality may not be immune in a very different locality, for plants often respond remarkably to changed environment, and one of the responses may be loss of resistance. It is even true that a strain usually resistant in a given locality may not be resistant during an unusual season in that same locality, a season which has resulted in some change in the structure of the plant.

The eventual stamping out of our most destructive diseases by suitable plant-breeding may be looked forward to with confidence. The selection and pedigreeing of immune individuals will secure the result, not once for all time or for all localities, but the variations are so numerous that resistant plants will be available at all times and for all localities. Whenever disease appears, and especially if it is virulent, immune individuals can be detected and pedigreed.

SUMMARY

The control of disease by fungicides or any other method of treatment is laborious and usually very uncertain; and, in many cases, as in most soil infections, it is impossible. To kill a fungus after it has attacked a plant is merely to check the disease, and not to eliminate it.

The final elimination of diseases will be attained when disease-resistant races of all plants are obtained. This is possible by the selection of plants found to be immune in the presence of a disease that is destroying other plants, and pedigreeing them for an immune race.

The first attempt to secure disease-resistant races is in connection with the most uncontrollable diseases, such as those from certain soil infections. Diseases which have been brought under good control by the use of fungicides can be allowed to wait.

Immunity depends upon a structure that forbids the entrance of a parasite, or upon a metabolism that does not furnish the appropriate food or that may include a toxin for the fungus. These structures and products vary with the condition of a plant, so that an immune race may not always remain immune in different localities, or in different seasons.

There will always be an opportunity to pedigree for immune races whenever and wherever a disease appears; and this continuous application of pedigree culture for immunity should ultimately result in the elimination of any disease anywhere. At least it may result in the periodic elimination of diseases.

CHAPTER XV

FORESTRY

Forestry has become so extensive and varied a subject that it is not easy to define. When public attention in this country was first directed to it, it awakened what may be called a sentimental response. Trees and forests appealed to many as features of the earth's surface that ought to be preserved, much as notable works of art should be preserved. The ruthless destruction produced by the pioneer backwoodsman and by the lumber camps came to be regarded as nothing short of vandalism. There is enough in this sentiment to justify solicitude for the preservation of forests, just as national and state parks are set aside to preserve a natural topography. But the practical aspects of forestry began to appear so conspicuous that soon it became an economic subject of the first importance. It is not so much a science as an art, but it is the practical application of several sciences, chief among which is botany.

In its broadest sense, forestry means the care of forests, but this includes many things to care for, and many things in view. It does not mean a kind of preservation which amounts to miserly hoarding; it means use as well as preservation, in fact, the freest possible use consistent with preservation. It does not mean merely the care of forests already existing, but also the replacing of destroyed forests, and the development of forests on areas where none exist naturally. The two chief purposes of this care are to maintain forests as the source of products necessary to human welfare, and as a check to floods that carry off soil. The latter purpose explains the numerous forest reservations upon important watersheds. In other words, a forest represents an enormously important crop, which must continue to be produced, and also a very important barrier to soil destruction. Connected with the use of a forest in such a way that it will continue to be useful, is the whole subject of the effective handling of the crop for its varied uses. It is evident that forestry has become a very complex subject, based upon scientific knowledge, and extending into a great plexus of practical operations.

The general scientific background of forestry is the natural development of a forest, which may be outlined in a general way as follows. Plants are not scattered at random over the surface of the earth, but are organized into definite associations, determined by the conditions for plant growth. It is recognized, for example, that there are forests, prairies, plains, and swamps, each one of which represents an association of plants that characterizes it. Into each association certain plants are admitted, and from each association certain plants are excluded; that is, we have come to recognize that certain plants are naturally associated because they grow in the same conditions. Any set of conditions for plants is said to be a *habitat,* and each kind of habitat has its own peculiar association of plants. Of course, certain plants can live in a considerable range of habitats.

The most important fact in reference to a plant association is that it is not permanent on a given area. In general, when a plant association lives for a time upon an area, that area becomes increasingly unfavorable to it, until gradually it is succeeded by another plant association. Almost any plant association finally makes conditions unfit for itself, and at the same time more fit for some other association. This succession of plant associations may be illustrated by a succession of human communities. Pioneer conditions bring together a characteristic association of individuals, but the conditions do not remain pioneer, and become favorable for another association of individuals; and this kind of succession may go on until the series of associations can be traced from the pioneer association to the metropolitan association. This means that each plant association can reveal the succession of associations that preceded it, and also the succession of associations that will succeed it. In other words, the most important thing in an association is the history and the prophecy it contains.

It is evident that there may be many kinds of succession, dependent upon the habitat. The start may be made on bare rock, on sand, on clay, in a swamp, and then each kind of succession will follow. It is also evident that the succession cannot go on indefinitely, but that some final association will be reached, which is called the climax association for that region. In general, some type of forest is the climax association, but there are obvious reasons why that type cannot be reached in certain regions.

A single case of forest succession will serve to illustrate not only the general meaning of succession, but also the facts that must be considered in any effective study of forestry. One of the best known forest regions is the white pine region of northern Michigan, from which the trees have been swept with no thought of their continuance, and the evolution of this forest will indicate the forest problems in general.

The succession of plant associations which led up to the white pine forest started on sand, rock, clay, or in swamps, but the series beginning on a sandy beach will be used in the illustration. The first stage was the lower beach, washed by the summer waves, and therefore with no vegetation, but with an accumulation of sandy soil. The second stage was the middle beach, rising higher above the water, and therefore washed only by the larger winter waves. This freedom from waves during the summer permitted the growth of certain annual plants, whose bodies added some humus to the sand. The third stage was the fossil beach; that is, a beach that was once washed by the waves, but is now beyond their reach. This continual freedom from wave action permitted the growth of more plants, and therefore resulted in the accumulation of more humus; but the soil would still have looked rather bare, as the plants would not cover the surface. The fourth stage was made possible by the accumulation of humus, and it is called the heath stage, for plants of the heath

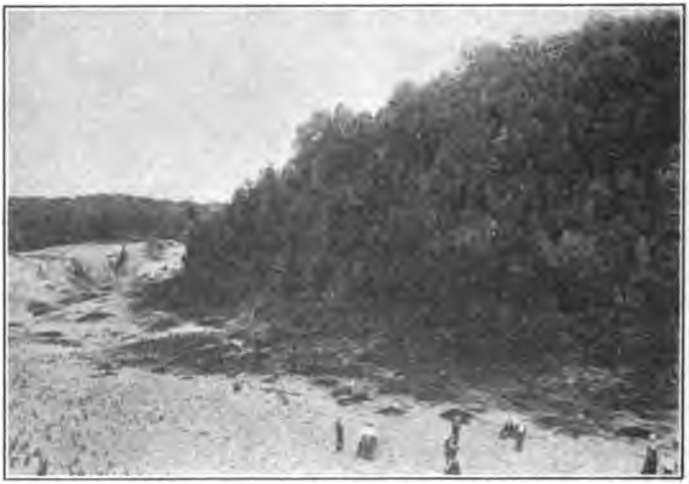

Fig. 91.—Evergreen forest encroaching on a heath, and the latter in turn encroaching on the fossil beach; North Manitou Island, Lake Michigan.—After Whitford.

family and their associates occupied the ground. At this stage, for the first time, the plants covered the ground so thickly that competition among individuals began.

With the further accumulation of humus the fifth stage became possible, that is, the pine forest stage.

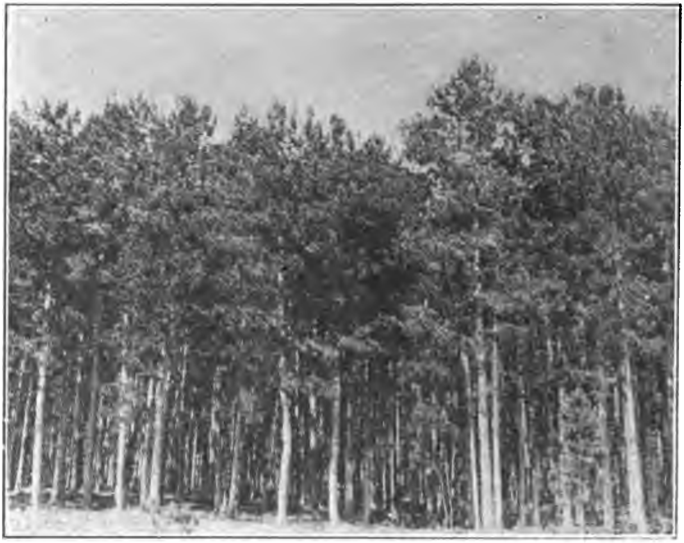

FIG. 92.—Pine forest on an old beach; near Marquette, Michigan.—After WHITFORD.

Gradually the pines invaded the heath (Figs. 91 and 92), first the jack pine, then the red pine, and finally the white pine. It was at this stage that men caught the succession and destroyed the pines. When a forest fire swept through the pine forest, it not only checked the succession but often set it back. If the fire were prolonged and intense, it not only destroyed trees, but also much of the humus, and in such a case the succession might be set back to the heath stage. This would mean a long accumulation of humus before the pine forest could come in again.

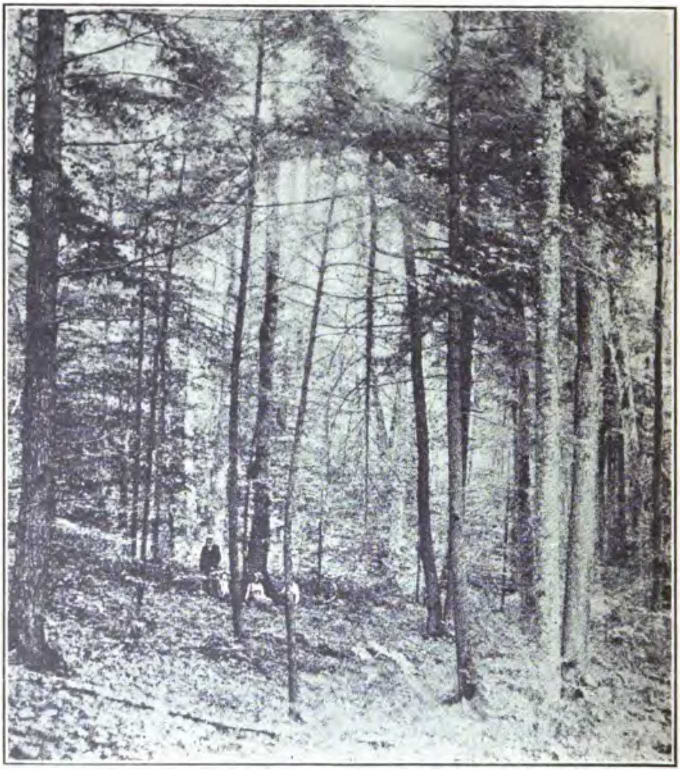

FIG. 93.—A maple-beech-hemlock forest; North Manitou Island, Lake Michigan.—After WHITFORD.

But the important fact is that the white pine forest is not the climax forest for that region, for it has the curious habit of what may be called race suicide. Its seeds do not germinate well and its seedlings do not thrive in the shade, so that when a deeply shaded white pine forest is established it cannot propagate itself. But this shade is favorable to the seeds and seedlings of the maple and beech, and therefore these trees gradually supplant the white pine, and the maple-beech forest is the climax association for that region (Fig. 93). It follows that the problem of forestry in the white pine region is not merely a fight against the devastation of man, but more fundamentally a fight against the race suicide of the white pine and against the encroachment of the hard-wood trees.

This is an illustration of but a single forest succession, out of a great many that forestry must recognize. For example, in Oregon and Washington, where the conifer forests are so conspicuous, they are of the climax type, and there is no danger of an invasion by hard-wood trees. The conifers of that region do not commit race suicide, and the deciduous trees are not favored by the winter rains and dry summers of that region.

After understanding the conditions that determine the presence of a forest and the kind of forest, it is necessary to realize the general character of a forest. Forests in general are either pure or mixed. A pure

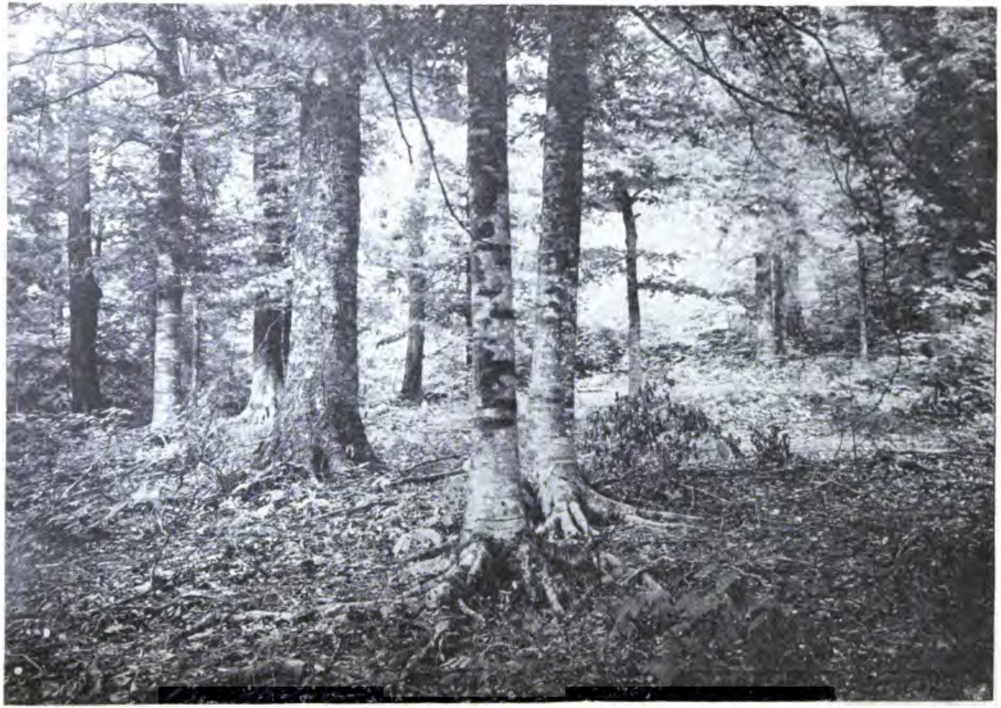

FIG. 94.—A beech forest in southern Indiana; a pure, dark forest.

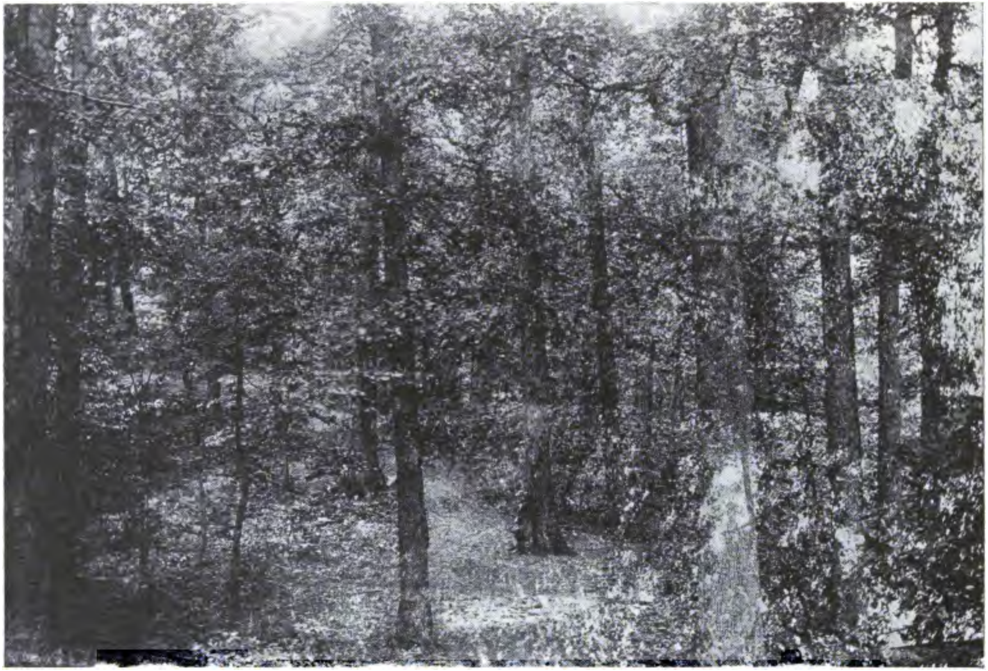

FIG. 95.—An oak forest in Tennessee; a pure and light forest, with undergrowth.

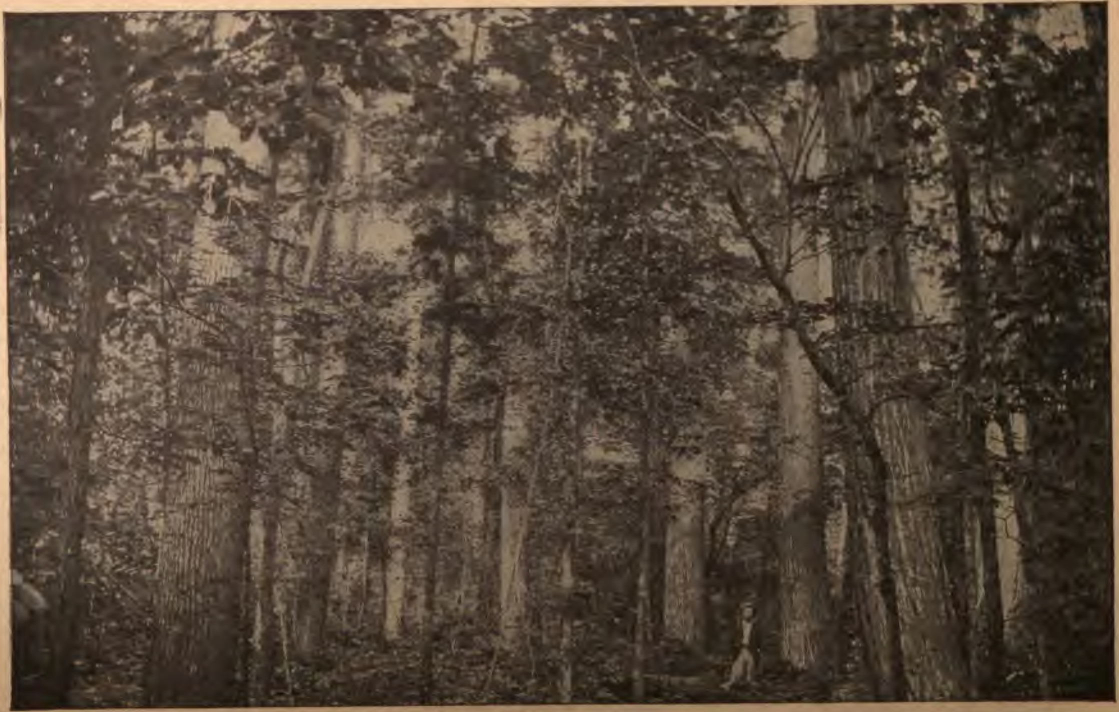

FIG. 96.—A chestnut forest in the mountains of Tennessee; an almost pure forest of large trees.

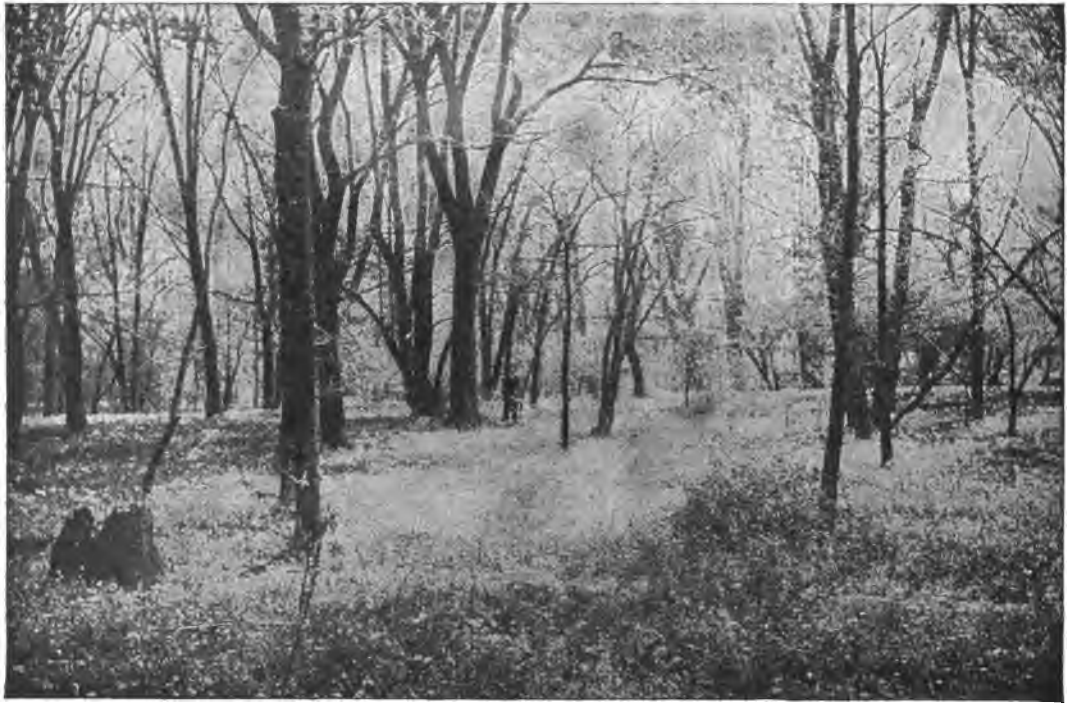

FIG. 97.—River bottom forest; a mixed forest (basswood, elm, etc.).

forest is one in which all the trees, or a large majority of them, are of the same kind (Figs. 94-96), while a mixed forest is one in which there are various kinds of trees (Fig. 97). There are three parts of a forest to be considered in forestry: (1) the canopy, (2) the forest floor, and (3) the character of the tree trunks, which represent the mass of wood that constitutes the crop.

The canopy is made up of the interlacing crowns of trees, and it must be kept as uniform as possible. The value of the wood depends upon this, for a good canopy causes the lower branches to be shed while they are small, and as a result the trunk is clean and free from knots. In the formation of a forest the forester sees to it that the canopy rises as the trees grow. In a pure forest a uniform canopy can be managed easily, but in a mixed forest the canopy is a more complex problem, for the different kinds of trees hold different relations to the light, some needing less light than others. In such a case the canopy is developed in stories, in accordance with the light needs of the different trees. The canopy serves several purposes in the economy of the forest. It manufactures the carbohydrate food for the trees; it shades the forest floor, and thus prevents the development of undergrowth; it checks the drying out of the soil, and shields the soil from dashing rains; it also enriches the soil with its leaf litter, making the forest soil the best of soils.

The forest floor is not merely the surface of the soil, but also the whole soil region in which the trees are rooted. This is usually deep and rich, but, more than all, the humus gives it the physical properties of a sponge in receiving and retaining water.

The character of the tree trunks is studied, not only to insure freedom from lower limbs by means of a suitable canopy, but also for the development of wood. Each tree has a period of development, during which it adds annually to its wood mass enough to pay for the room and care it requires; but eventually it reaches a stage when it is not making enough wood "to pay for its keep." The time to use a tree, therefore, is when it has reached its maximum wood production and has not yet begun to decline.

Forests not only build up and enrich the soil, but they also fix the soil—a fact of great importance, especially in a hilly country. The interlacing roots grasp the soil so that roots and soil are knit together in a mass that resists erosion. It can be observed that hillsides from which the forests have been removed soon become gullied and stripped of soil. This protection against erosion serves not only for the soil in which the forest grows, but also for the soil of the fields at the lower levels.

Forest soil holds water so persistently that heavy rains do not run off quickly and produce floods as they do in bare regions. It is often remarked that streams that had a steady flow when a region was first settled have become alternately flooded and dry since the forests were removed. Therefore the forest-covered soil not only prevents erosion of soil and flooded streams, but provides also a steady supply of water to the streams.

The establishment of a forest where one does not exist, or the making over of an inferior forest, involves so many technical details that it would be foreign to the purpose of this book to enumerate them. The technic of forest formation, as these processes are called, must be learned from the special treatises devoted to this subject, and from experience, but some idea of the things involved will lead to an appreciation of one phase of the work of a forester.

Sometimes the soil must be reclaimed by draining if it is swampy, and by putting it into better physical condition if necessary. Great judgment must be used in the selection of trees for a given region, and in the decision whether it is better to establish a pure or mixed forest. The seed used must be tested thoroughly for quality, and the care of seedlings is full of details. In general, the germination of seeds and the care of seedlings are best provided for in reliable nurseries. In making over a forest of inferior quality, the problem is to give seedlings a chance to grow, and to replace the old and inferior trees by young and vigorous ones. Of course, each forest has its own problems, but enough has

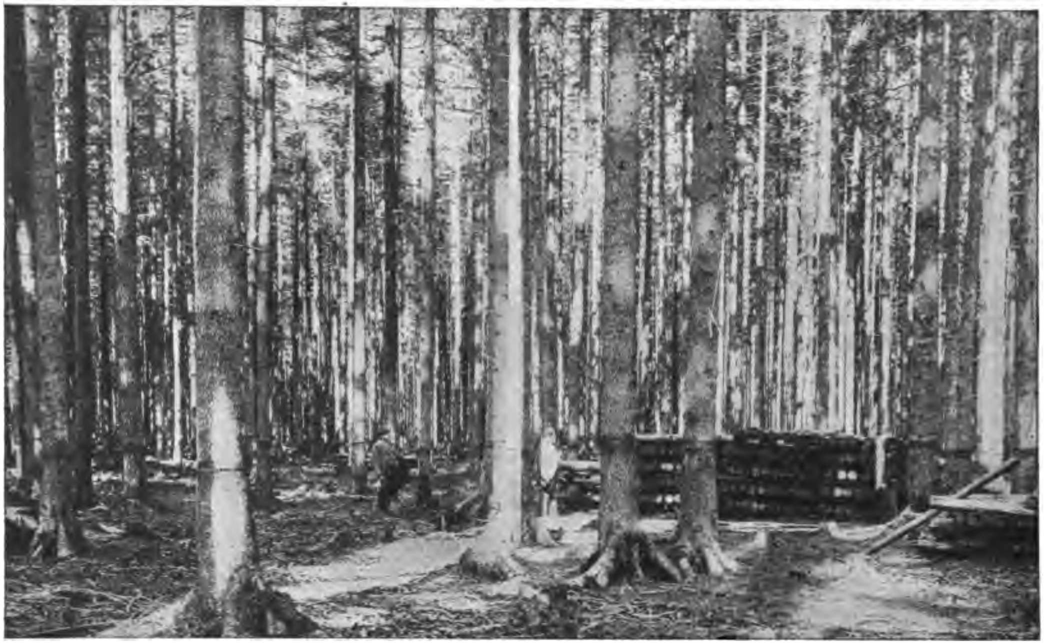

FIG. 98.—A spruce forest in Germany which has been frequently thinned.—After GIFFORD.

been stated to indicate how a uniform stand may be secured in making or reclaiming a forest.

The care of an established forest means keeping it in good condition. ''Cleaning'' a forest means the removal of useless trees, useless because they are dead, or injured, or old, or unpromising, and the removal of other plants and brush that interfere with the proper condition of the forest floor. ''Thinning'' a forest means the removal of certain trees to prevent the trees from interfering with one another (Fig. 98). This interference is mostly a question of an overcrowded canopy, for the crowns must expand freely and interlace, but must not interfere with one another's development. Sometimes pruning is helpful, but this is not practicable in a large forest as a general performance. The advantage of a forest growth in the production of wood as contrasted with isolated trees should be understood. A tree ''in the open'' is often thought of as the best developed tree, which may be true so far as its general appearance is concerned; it seems to satisfy best our idea of how a tree should look; but if a tree is expected to produce wood of good quality it must be associated with other trees so that a good canopy is developed. A tree in the open produces more wood, but it is poorer in quality, because the lower limbs are allowed to develop and the wood is full of knots.

The protection of forests is one of the most difficult problems of forestry, for it involves the passing of laws and their enforcement, and the hearty coöperation of communities. This is especially true of protection against fire, which is the greatest enemy of the American forest, and is mostly the result of ignorance, carelessness, or indifference. The fierce fires in the white pine regions of Michigan, Wisconsin, and Minnesota have become familiar, and sometimes they involve extensive destruction, not only of valuable trees, but also of human lives. An investigation of the causes of these recurring forest fires has shown that the escape of sparks from passing locomotives is the chief cause. It is evident that this cause of fires can be controlled if public sentiment becomes strong enough. Another prolific cause of fires comes from the carelessness of campers and hunters, a cause that is troublesome to check. Farmers often "clear the land" by fire, and carelessness or lack of judgment may result in permitting the fire to extend into the adjacent forest. The effect of a fire differs in its destructiveness. It may involve only the canopy; it may run over the surface of the soil; or it may be fierce enough to burn the humus of the soil. In any case, the forest is crippled, and in the last case, not only are the trees destroyed, but the soil is no longer fit for forest growth.

The danger of hard freezing is also to be considered, for it may kill the buds, crack the stems, and upheave the young plants. Frost cracks in lumber show that damage from this cause is often serious. The trees cannot be protected from such a danger completely, but a dense canopy reduces the danger, and a thick litter of decaying leaves on the forest floor is still further protection. Damage is also done by violent winds, hail storms, sleet, and snow, but these are the accidents of nature that involve only a repair of the damage.

There are many insects that are very destructive to trees, because they bore into the wood or eat the leaves. The gipsy moth has become famous for its leaf-destroying powers. The best protection against insects is to encourage their enemies; a forest full of birds, toads, snakes, etc., is well protected against destructive insects. The need for such protection justifies the exclusion of hunters from various forests under cultivation, especially the men who shoot at everything. The problem of grazing animals in a forest is a mixed one. These animals are usually sheep, and up to a certain number they may not be injurious, and may even be helpful, but in large numbers they are injurious, being not only grazing but browsing animals.

The dangers to forests from plant diseases were considered in a previous chapter, which deals with plant diseases in general.

It is a surprise to many to discover the number of uses to which forest trees are put. Most people probably think of forests only as a source of lumber, so far as their commercial use is concerned. It is true that

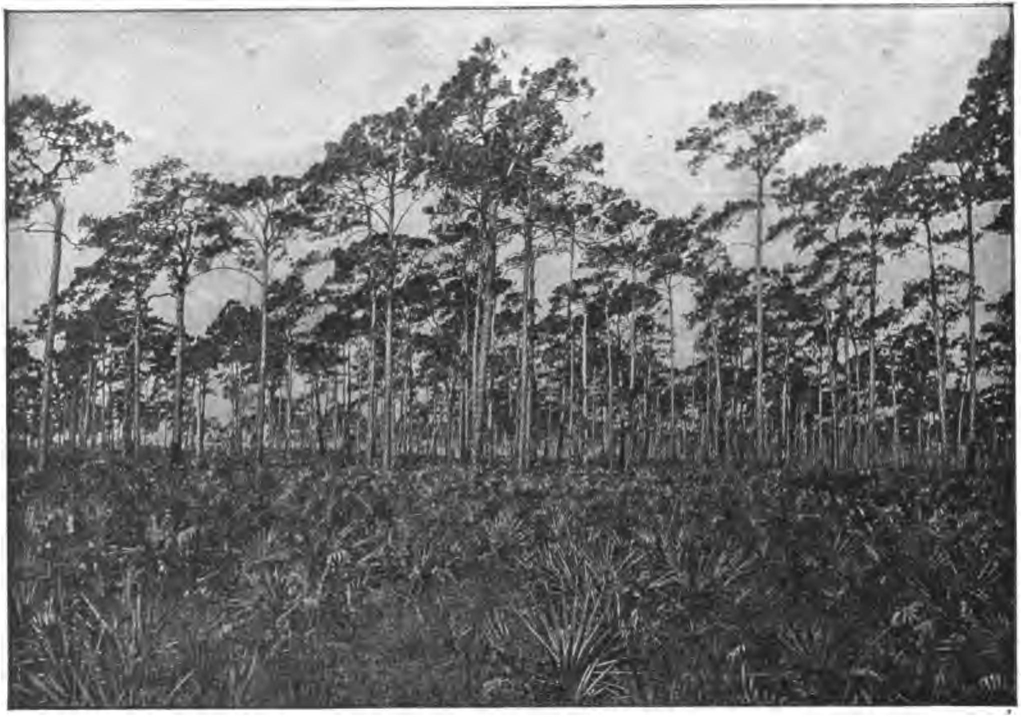

FIG. 99.—A grove of southern pines.—After SCHIMPER.

lumber is the conspicuous product, and it is known that this lumber is put to endless uses. For this purpose trees are grouped as "soft woods" (pine, spruce, hemlock, cedar, etc.), and "hard woods" (oak, walnut, hickory, cherry, ash, maple, elm, etc.). The lumber industry in soft woods may be used as an illustration. The most prized soft wood is the white pine, and the important white pine states are Michigan, Wisconsin, and Minnesota. This valuable tree has been harvested so recklessly that it has now approached dangerously near the point of extinction as a commercial source of lumber. In the South the yellow pine is the great soft wood (Fig. 99). The third great region for soft wood lumber is in the Northwest, in the Douglas spruce and redwood forests of the Pacific slope.

The use of wood pulp in the manufacture of paper is a tremendous industry. The most commonly used wood is spruce, and the process consists in grinding the wood into pulp and pressing it into paper. This pressed pulp, aside from paper manufacture, is used in the manufacture of a great variety of articles, as buckets, doors, and even wheels. In the manufacture of paper it is estimated that one ton of paper pulp is produced by one and a half cords of spruce wood. The amount of this paper used by newspapers is enormous. It has been estimated that one large newspaper in New York City uses in one year all the spruce grown on 16,000 acres of land as spruce naturally grows. If this amount be multiplied so as to include all the newspapers, it is evident that the supply of spruce will fail speedily. Of course, other woods can be used for the same purpose, Carolina poplar making a very good wood pulp.

The pines are used as a source of resin and turpentine, which occur as "crude resin" in the ducts of the wood. The largest supply of this product comes from the pine woods of the South, but in collecting it the trees are so handled that they are destroyed. In France the product is obtained without destroying the trees, and unless some such method is introduced in the Southern pineries the resin industry is doomed to destruction.

The bark of certain trees is also used as a source of tannic acid for tanning leather. In Europe oaks are extensively propagated for this purpose, but in the United States hemlock bark is used. With our usual recklessness the trees are practically destroyed in securing the bark, so that now a large amount of our tannin comes from South American woods.

The destructive distillation of woods yields a remarkable variety of products that need not be enumerated, chief among which are alcohol, acetic acid, and tar. In every case after the desired product has been driven off by distillation charcoal is left.

Any consideration of the products of trees must include maple sugar and syrup. This is said to be the

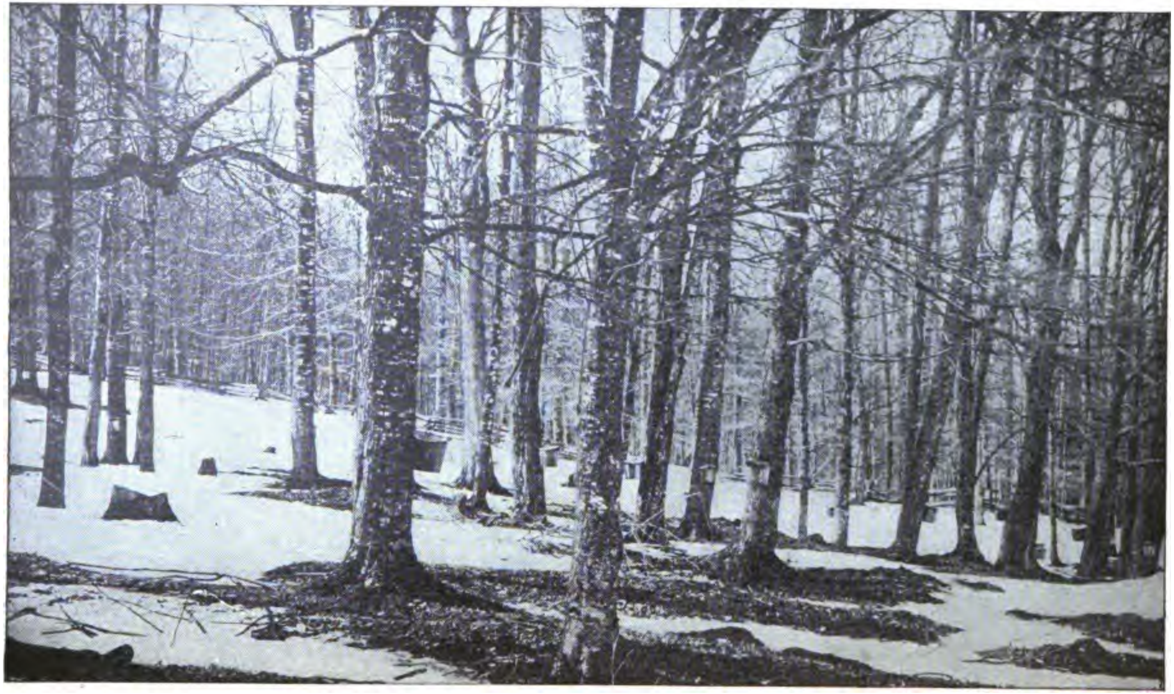

FIG. 100.—A sugar maple forest in northern New York.—After GIFFORD.

only forest industry that has been developed on a scientific basis (Fig. 100). It is an American industry, and when it is known that over 5,000,000 pounds of sugar and 3,000,000 gallons of syrup are produced each year it can be appreciated that the industry is a large one.

Another use of forest products has yet to be developed in the United States. In Europe every twig is used; that is, the forest refuse which we destroy as brush is all utilized. To use this material seems to the American a waste of time, involving an amount of labor that is not paid for by the result; but since many uses for forest refuse have been developed in European countries there is no reason why some of them may not be introduced here.

The great importance of exercising some control over forests has led the national Government to adopt a system of forest reservations, which are under its care. To a certain extent states have done the same thing. It is not the purpose of the Government to withdraw these forests from use, but rather to supervise their use, so that they may continue to be productive. Furthermore, some forests are reserved by the Government, not so much for the sake of a continuous lumber supply as to protect certain regions from floods and soil destruction.

Although not coming strictly under the head of forestry, a brief consideration of tree culture along streets is a subject of great practical interest. The streets fitted for tree-planting usually provide a planting strip between the sidewalk and curb, and in a very wide street a parking strip in the middle is often seen. Much street-planting has been done independently by the owners of different lots, so that the trees are of various kinds, and the result is a ragged appearance. If possible, a reasonable continuity in the kind of tree used improves the appearance of a street very much. Not only should the trees be of the same kind, but their spacing should be uniform, and this differs for different trees. The spacing should be a little larger than the natural spread of a tree; for example, the following spacings are recommended; white elm, fifty feet; maple, forty to forty-five feet; linden, forty feet; Carolina poplar, thirty feet.

The selection of trees is important, and the judgment of people will vary. The primary choice is between a fast-growing tree and a slow-growing tree. The former brings results quicker, which means beauty and shade, but it is usually a short-lived and brittle tree. The latter develops beauty and shade very slowly, but it is usually longer-lived and tougher. It would seem wise to select for city streets the slow-growing and long-lived trees, the most popular of which is the white or American elm. The rapid growing trees which impatient people select are usually Carolina poplar, willow, box elder, or silver maple.

The space for soil preparation is very restricted, so that instead of breaking up the soil in the usual way for a crop, large holes are dug and filled with proper soil, which in this case means a pulverized soil, thoroughly mixed with fine manure. More care must be taken to see that there is proper drainage, and often a tile drain has to be laid. The young trees are usually obtained from a nursery, and before they are "set" they are pruned, so that the stem system may balance better the more or less injured root system. In case the root system is complete no trimming is necessary, but it would be a rare amount of care that could transplant a young tree without injuring the roots more or less. Of course, trees must be transplanted while they are dormant, and this means either a spring planting or fall planting, the former being the better. Sometimes very large trees are transplanted, but the larger the tree the greater the danger.

In observing most street trees, one might infer that after the trees are planted they need no attention. While they need little attention after they are full grown, the young and growing trees cannot be neglected. Perhaps the greatest cause of failure in the growing of street trees is the poor physical condition of the soil. It is evident that the soil must be kept in good condition, and since the feeding-ground of street trees is much restricted, certain fertilizers are of great help.

There are many sources of injury to street trees, due to city conditions. Smoke poured out abundantly from smoke stacks, and gas from leaking pipes escaping into the soil about the roots are common causes of dead and dying trees seen along the streets. Electric linemen are often reckless in chopping out branches to clear the way for wires. Trees are often also seen to be used for anchoring guy-ropes. Regrading streets often destroys trees ruthlessly and needlessly. Ignorant pruning probably destroys more trees than any other danger, not only because the pruning is wrong, but also because the wounds are not cared for. The old days of using trees for hitching-posts and subjecting them to wounds from horse bites are nearly past. Of course, storms are to be reckoned with, and a sheeting of ice breaks many twigs and often large limbs. The best protection against damage from such storms is to select for street trees those that are not brittle. The Carolina poplar, willow, and silver-maple are notably brittle, and after a storm the ground beneath them is strewn with a litter of branches.

SUMMARY

Forestry means in general the care of forests, the two purposes being to maintain them as a source of necessary products, and as a check to floods that carry off soil. It also includes the making over of inferior forests, the establishment of forests where they do not exist at present, the use of forests so far as it is consistent with their preservation, and the handling of the crop for its various purposes.

The scientific background of forestry is a knowledge of the succession of plant associations that lead up to a forest. This enables the forester to realize the type of forest that belongs to a given habitat, and also whether the climax type has been reached. It is this scientific background that has developed the knowledge, for example, that the white pine forest is not the climax type for its region, but will be replaced by the beech-maple forest if left alone. In this case, therefore, forestry is not only a fight against devastation by man, but also against nature.

The three parts of a forest to be considered are the *canopy,* made up of the interlacing crowns of trees, and which manufactures food and protects and enriches the forest soil; the *forest floor,* which is the soil in which the trees are rooted, and which should have the physical properties of a sponge; and the *character of the tree trunks,* which produce the crop.

Forests not only furnish lumber and other products, and build up the soil, but they also fix soil, a fact of great importance, especially in hilly countries. It is for this purpose that many Government forest reservations include important watersheds.

The protection of forests against man is one of the most difficult problems of forestry, for it involves the passing of laws and community coöperation in their enforcement.

The uses to which forest trees are put are surprisingly numerous, as the following common products would indicate: lumber, wood pulp for the manufacture of paper, resin and turpentine, tannic acid, alcohol, acetic acid, tar, maple syrup, etc.

CHAPTER XVI

THE SEARCH FOR NEW PLANTS

It is a natural tendency for the crop-producers of a country to restrict themselves to a limited range of plants. The cultivation of certain plants has been inherited by each nation, and the taste of the people has become adjusted to these plants. As cultivation continues and becomes more scientific, great improvements are made in the plants of a country, so that crops become more certain, more abundant, and of higher grade. This provincialism in crops may not be a serious handicap in an isolated country which is compelled to be sufficient unto itself in the matter of food-production. This situation for countries is just what it once was for families, when they were independent units and did not depend for subsistence on other families. This situation has not only changed for families, but also for countries. No civilized country is isolated now, and the crop-producer in the United States is coming rapidly into competition with the crop-producers of the world.

Another important consideration in connection with provincial crop-production in the United States is the great diversity of soil and climate. A limited number of plants cannot possibly represent the maximum production for all regions of the United States, extending as they do from high temperate altitudes to the subtropics, and from deep, well-watered soils to deserts. In fact, all the conditions for plant growth in the world are more nearly represented in the United States than is generally appreciated. It is evident that, if this country is to remain strong in a world-competition for food-production, it must find plants of maximum yield for every plant habitat. When one realizes the thousands of different kinds of native plants that inhabit the United States, he appreciates how diversified must be the conditions for plant growth. This ought to suggest as great a diversity of cultivated plants as possible in order to increase the total production. To accomplish this will require something more than multiplying races of the comparatively few plants now cultivated in the United States. It will require a study of the crops of the world, and the introduction of such foreign plants as will meet certain conditions better than those we are now cultivating. In other words, we must encourage the immigration of useful plants, just as we have built up a strong nation by the encouragement of human immigration.

The value of the introduction of desirable foreign plants is not to be measured by the number of species introduced. With the methods of plant-breeding that have been developed, a single new species may become the origin of a large number of races adapted to our varying conditions and developing qualities, both in kind and in variety, unknown in the regions of original cultivation. A desirable form, therefore, may become the parent of a large progeny of desirable forms.

With some such view as to the future needs of this country, in 1897 the United States Department of Agriculture established the "Office of Foreign Seed and Plant Introduction." Under the direction of this Office, explorers have looked for useful plants in various parts of the world, and special investigators have studied the production of important foreign crops. An immense amount of information has been secured and made available, and to make this information of service to the crop-producers of this country is the purpose of this Office.

The introduction of new crops is a slow process, for it must overcome prejudice, training, and sometimes taste. Furthermore, the new crop must be demonstrated to be a useful one; it must be made familiar to crop-producers, and it must supply a growing demand. To accomplish these things the Office of Seed and Plant Introduction during the seventeen years of its existence has introduced for trial in this country over 40,000 varieties of foreign plants. It is not expected that all introductions will be found useful, or will appeal to the American taste, but they represent plants used in foreign countries that deserve to be tested in this country.

The general purpose of the Department of Agriculture in maintaining such work has been stated to be "to help find the plant which will produce the best results of any that can be grown, on every acre of land in the United States." An amplified statement of this purpose is well expressed in the following extract from an address given by Mr. David Fairchild, Agricultural Explorer, in charge of foreign seed and plant introduction:

> "Carried on as a government policy over a long series of years, what will be the result of this plant-introduction work? To my mind there can be no question that it will be one of the great agents in the diversification of our agriculture and help lessen the losses which occur by the shifting of farm industries from one region to another. It is in line with the development of the human race, which is moving from the one-food basis of the savage toward a multiple food standard. It will lead to substitution in our foods of better for inferior things. It will result in the creation of those natural plant monopolies upon which the agricultural wealth of a country should rest, monopolies such as have made the peasantry of France so well-to-do. It will lead to the utilization of land by that crop which is best able to create food or other valuable material on that land. It will lead to the substitution of the tree crops for annual crops wherever they are of advantage. It will assist in the utilization of waste lands all over the country. It will help make the roadsides, city streets, parks, and yards more attractive, as it has made

them in England, by the discovery of ornamental plants adapted to cultivation here. It will prepare the young horticulturists of America for the opportunities of the tropics which are opening with such remarkable rapidity and which are sure to attract American capital and enterprise on a gigantic scale. It will help to enlighten the American farmer on what the other farmers of the world are doing, and furnish him with material with which to compete with them in a host of lines."

When an explorer or an investigator introduces a new crop plant for trial, it is grown under experimental control as the first test. If it seems promising, it is distributed among certain gardens and experimenters for further testing. Finally, it may be sent to everyone who is willing to experiment with it. In this coöperative way a new crop plant may gradually find a place among our old ones, and it is the best kind of training for a host of scattered experimenters to share in testing the possibilities of a new plant. Of course, it has been necessary for the Department to establish certain experimental gardens of its own, well distributed as to climate and soil conditions, in which the initial propagation and sometimes the more or less continuous propagation of foreign crop plants can be studied; in which also the desirable plants can be multiplied in sufficient quantity for distribution. At present six experimental gardens or propagating stations are established, as follows: Chico, California; Brooksville and Miami, Florida; Yarrow (near Rockville), Maryland; Brownsville, Texas; and Mandan, North Dakota.

A list of the plants that have been introduced, and that either have become established among our older crops or bid fair to become so, would be a long one, and yet this is but a small beginning of the possibilities that lie in the future extension of this work. A very few illustrations will show the nature and importance of the introductions.

Even magazine literature has familiarized the public with the value of such introductions as the Durum wheat from the Mediterranean and Black Sea region, which has done so much toward solving the problem of a good drought-resistant wheat; the Japanese rice, which has enormously increased our output of rice; and the alfalfas from Siberia, which have revolutionized forage production, especially in the western states.

One of the most noteworthy introductions is the Oriental mango, which is often said to be the finest fruit in the world; certainly it is one of the great fruits (Fig. 101). Its value in India is so highly esteemed that it has been made a sacred fruit. There are endless varieties of mango, of all flavors and textures and sizes. These are now being grown in Florida, Porto Rico, and Hawaii, and the results show that the American demand for this fruit will keep pace with any increasing production.

A very important new plant is the date palm, which is one of the oldest cultivated plants in the world (Fig. 102). It is said to be the plant that enabled the Arabs to live in the desert. The plant is remarkable for its endurance of conditions that make most crop

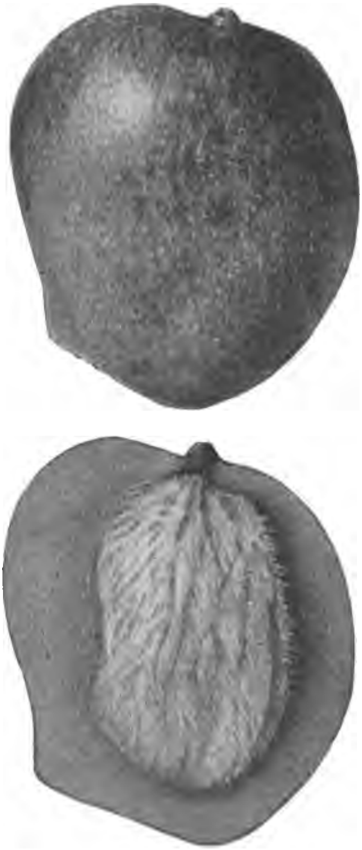

FIG. 101—Peters' mango.—Year Book, Dept. Agri.

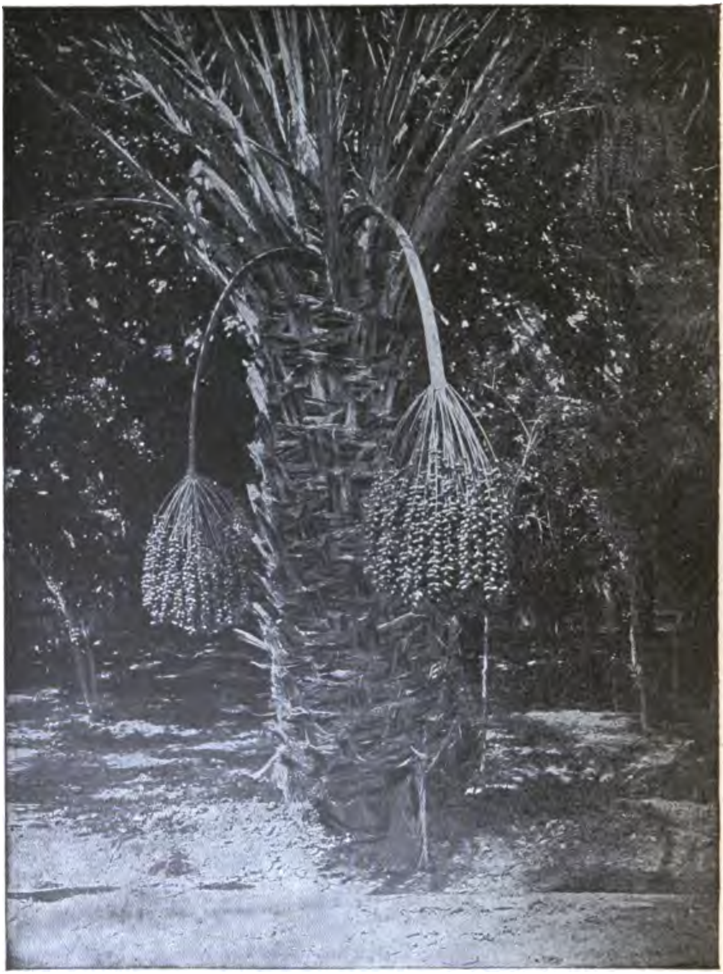

FIG. 102.—Base of a date palm, showing two fruit clusters.

plants impossible. It can thrive in alkaline soil, so salty that no other crop plant can grow. It cannot only live in the warmest temperature of the world, but it can also stand a slight frost. The yield of fruit by a single tree is enormous, reaching in this country as much as one hundred and thirty pounds. It took much work in many countries, by many men, through many years, to establish the date palm in our arid Southwest; but now over one hundred varieties are growing in six coöperative date gardens in Texas, Arizona, and California, and are being distributed to prospective growers. It has been estimated that a profit of one hundred and fifty dollars an acre is to

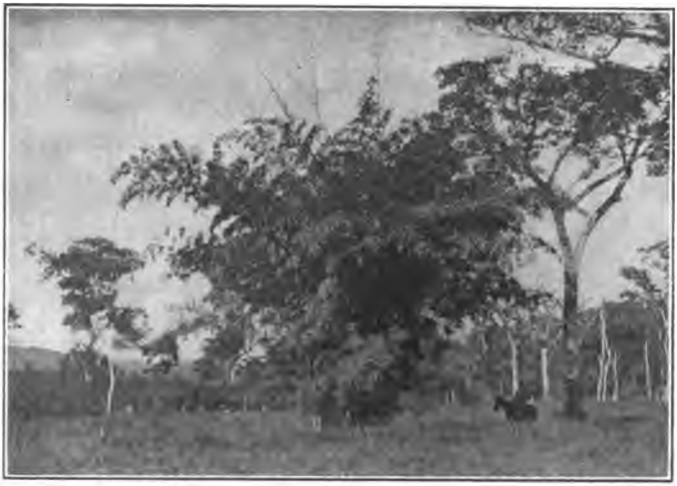

Fig. 103.—Timber bamboo.—Photograph by Land.

be expected from a well-managed date plantation, and it must be remembered that the acres referred to are such as would ordinarily be called a desert.

Another conspicuous fruit that is coming into notice is the persimmon, the discovery being made that the Oriental (especially Japanese) persimmon is a fruit of first importance. Our own slowness in recognizing the value of this fruit has been due to our acquaintance with its very inferior representative in this country.

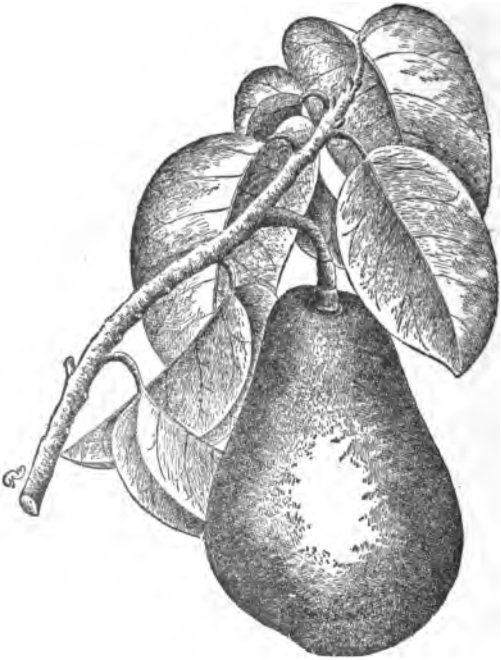

FIG. 104.—Avocado (alligator pear).—After BAILEY.

The improvement of the persimmon, therefore, has come to be another current problem.

One of the most recent introductions has been the Oriental timber bamboo (Fig. 103). Anyone who has traveled in the Orient must have been impressed by the extensive use made of this plant. Its lightness and durability make it singularly efficient for many purposes. It is said that there is no plant in the world that is put to so many uses as the bamboo. Groves of these are now being established in northern Florida and Louisiana, and the commercial possibilities of this plant in the Southern States are well worth the effort to extend its cultivation.

To illustrate the range of introductions that are being made, and that give promise of great usefulness, the following may be mentioned:

The seedless grapes of Italy and Greece are already being included among our table grapes.

The dasheen, which is a root crop related to the Hawaiian taro, will probably rival the potato as a food producer. The significance of this crop lies in the fact that it is suitable for cultivation in the Southern States in lands that are too moist for the potato.

The introduction of avocados (alligator pears), natives of the West Indies and of the American tropics from Mexico to Peru and Brazil, has established a place for this notable fruit of the American tropics among the fruits of California and Florida (Fig. 104).

The Smyrna fig has now become established as an industry on the Pacific coast.

The introduction of a wild peach stock from China, which is hardy in the Middle Western States, has made peach culture possible in regions where it was prevented before by frosts.

The introduction of the Chinese wood-oil tree, whose nuts yield the best varnish oil, has made it possible to introduce a new crop in the Gulf States for cheap lands that have heretofore been producing little or nothing.

In the list of recent importations of foreign plants, expected to prove useful in this country, the following items appear:

In 1907 there were twenty-three varieties of soy bean in this country, while a recent Bulletin reports that three hundred varieties have been imported from every part of the world and tested. Since the soy bean is a most valuable forage crop for the Southern States, the significance of these importations is apparent.

Recently sixty-four varieties of tobacco have been introduced, in the hope of securing disease-resistant races.

From South America two hundred and forty-eight races of potato have been brought to take part in experiments to multiply the useful races of this fundamentally important crop.

To develop rust-resistant races of asparagus, thirty-five varieties have been imported recently.

The greatest number of recent importations have been varieties of alfalfa and its allies, the world having been ransacked for suitable races of this most important forage plant for all parts of the United States.

Races of cotton have been brought from Egypt to improve our production of this important staple.

Numerous races of forage grasses have been imported from Africa which promise to revolutionize the production of hay throughout the Southern States. Notable among these imported forage grasses are the strains of Soudan grass.

These illustrations will serve to indicate the organized effort that is being made to secure new plants; to utilize the experience of all nations cultivating plants; and to bring together upon our diversified area all plants that will either increase or vary our products.

SUMMARY

The Office of Foreign Seed and Plant Introduction of the Department of Agriculture, established in 1897, has undertaken the business of introducing into the United States plants from all parts of the world which may be of service in increasing and diversifying our plant products.

This country is restricting itself to a limited range of crop plants, resulting in a provincialism in food-production which is far from representing the maximum production for all parts of so extensive and diversified a country as the United States, which may well utilize plants from every part of the world.

It is not expected that all imported plants will prove to be useful; they must be tested, explained, and distributed. For this purpose the Government has established propagating stations in various parts of the country.

The importations that have already proved to be of great value are very numerous, supplying valuable plants for relatively sterile regions, improving productions in regions already under cultivation, supplying a much greater range of useful products, and securing new qualities for the old races.

The volume of importations is increasing each year, so that many thousands of foreign races are now under experimental study, each year adding to the list of those that prove to be valuable additions to our plant products.

CHAPTER XVII

WHAT THE GOVERNMENT IS DOING

In the preceding chapter, the work of the Government in searching the world for new plants was described. This is only one of the multifarious activities of the Bureau of Plant Industry. Those who are interested in plants should have some general conception of the organization of the Department of Agriculture. Among the aims of the Department, as stated by its recent secretary, are the following:

> To bring the scientist to the help of the people; to ascertain what imported crop plants might be produced in our own country; to search the world for grains, fruits, vegetables, grasses, and legumes that might be found useful here; to secure new varieties of plants by breeding and selection; and to control destructive diseases.

The scientific work of the Department is distributed among eight great divisions, mostly called "Bureaus," each with its chief and staff of investigators. These divisions are as follows: Weather Bureau, Bureau of Animal Industry, Bureau of Plant Industry, Forest Service, Bureau of Chemistry, Bureau of Soils, Bureau of Entomology, and Bureau of Biological Survey. The subject with which this book deals falls for the most part under the Bureau of Plant Industry. This great Bureau is a very complex organization, its scientific work being distributed among seven major divisions, each division being subdivided upon the basis of the particular type of investigations conducted. These main divisions are Pathology, Physiology, Technology, Horticulture, General Farming, Agronomy, and Seed and Plant Introduction and Distribution. An illustration of the subdivisions may be taken from those under Pathology and Physiology. Pathology includes divisions of bacterial diseases, diseases of fruits, diseases of forest trees, diseases of cotton, truck crops, etc. Physiology includes life history investigations, bionomic investigations, soil bacteria, water purification investigations, drug plant and general physiology investigations, and plant nutrition investigations. These names may not suggest the kind of work in every case, but they do suggest the effort to investigate the whole range of problems that bear any relation to agriculture. When it is known that under these seven major divisions there are approximately thirty subdivisions, each with its own staff of investigators, and that the Bureau of Plant Industry is only one of eight great bureaus under the Department of Agriculture, the extent and variety of the work of the Department for the benefit of agriculture may be somewhat appreciated.

In addition to the work done by the Department of Agriculture, there are sixty-six Agricultural Experiment Stations in the United States (including our insular possessions), where similar work is being carried on. It is evident that the total volume of work represented by these Government and State organizations is enormous, and that if the methods and results of agriculture are not improved each year it is not from lack of opportunities for investigation, but from lack of scientific insight on the part of investigators and those who are directing them. An immense amount of information in the form of Bulletins is being sent continuously to crop-producers, and it would be impossible to estimate the service that this has rendered.

In addition to these bulletins, the "Experiment Station Record" brings together in brief abstracts the significant work relating to agriculture from all parts of the world. To indicate the amount of such work that is being published, the "abstract number" of the record for April, 1914, may be used as an illustration, selecting in the main from the work of 1913, so far as plant-breeding is concerned. This number contains thirty-four titles on agricultural chemistry, forty-two on soils and fertilizers, twenty-one on agricultural botany, fifty-seven on field crops, sixteen on horticulture, thirteen on forestry, and fifty-four on plant diseases. These two hundred and thirty-seven titles are selected as deserving mention on account of their bearing upon the problems of agriculture.

A brief account of some of the work in plant-breeding undertaken by the Department of Agriculture will indicate more definitely the purposes in view and the results attained. The general statement may be made that almost every important crop is now under investigation. So far as plant-breeding is concerned the investigations have in view the improvement of existing varieties, the determination of the most suitable varieties for each region, the securing of the greatest resistance to drought and disease, and the development of the best agricultural methods.

Probably the first work in plant-breeding undertaken by the Government was the attempt by Webber and Swingle, almost twenty years ago, to produce a hardy orange, an attempt referred to in a preceding chapter. The hardy, but inferior, Japanese *Citrus trifoliata* was crossed with standard Florida oranges, and the result has been a number of forms called "citranges," some of which are proving to be of economic value (Fig. 63). They are adapted for growth in regions just outside the region of ordinary citrus culture, thus extending the area for the cultivation of citrus crops. Extensive breeding experiments with citranges are still being conducted, and there is every prospect that this new type of citrus fruit will become a permanent feature of our fruit production. It is claimed that the citranges will prove to be decidedly valuable as a substitute for lemons, and they can be cultivated in regions that are prohibitive to lemon culture.

Early in the history of the Bureau of Plant Industry, which was organized in 1898, maize, cotton, and tobacco were taken up for breeding work. These three important crops have now been under investigation long enough to make the results of such work evident and to indicate what may be accomplished with other crops.

Maize is our greatest crop, so that much attention has been given to its improvement. Ordinary methods of selection had not reached very satisfactory results. There had been developed a selection of ears based upon a number of ''points'' that a good ear should show. Private enterprise in this way had done much to increase the productiveness and improve the quality of maize. When, in 1901, the Bureau of Plant Industry began the series of investigations which are still being continued, it was soon discovered that ears selected on account of their good points did not necessarily result in a more productive or profitable crop. A better knowledge of the principles involved has been developed gradually, so that now crops can be more assured because of the development of races more resistant to drought, disease, and insects; can be more abundant than ever before; and are of far better quality. It was also discovered that there is no such thing as a uniform maize region, and that therefore there is no such thing as a uniform best variety. Great differences developed in different habitats, and much of the work of the Bureau has been directed toward a proper adjustment of varieties to habitats.

About the same time work with cotton was begun, emphasized by the necessity of solving the problem of the destructive boll-weevil. As in all such cases, one problem has opened up another, and the results of approximately fifteen years of work may be regarded as a report of progress rather than of final accomplishment; and still the progress has been remarkable. In this crop, also, an adjustment of varieties to habitats was found to be necessary, so that a given race of cotton is prescribed for a given habitat as being the most productive and the most profitable. It has also been found that any variety of cotton adapted to a given area may suffer serious deterioration by chance crossing with another variety. It follows that each region should be limited to a single variety. This calls for a new type of community action, for a single cotton planter who perversely uses a race other than that used by his neighbors may cause a deterioration of all the crops of the neighborhood. The variety most suitable for any area need not be a matter of varying opinion among the cotton planters, but may be referred to the Bureau of Plant Industry for a definite prescription. In the case of cotton, therefore, the methods used to maintain a variety are totally different from those used to secure new varieties. Such facts must be learned for all crops, and this knowledge can only be developed by a long series of breeding experiments.

The investigation of tobacco was started with the organization of the Bureau of Plant Industry, and has developed into an extensive and varied series of experiments, involving not only the races of tobacco but also its proper curing, and all matters relating to its handling. When the work began, the yield and the profit were comparatively small. This was found to be due to the cultivating of very mixed and undesirable forms. In fact, a field of tobacco was almost as conspicuous a mixture of different types as was the ordinary field of maize. Not only were the types mixed and poor, but the cultural methods were inadequate, such things as proper rotation, fertilizing, etc., being practically unknown. All this has been changed. The old types have been isolated from mixtures and improved by selection; new and more productive types have been produced by breeding; and foreign varieties have been introduced and made to contribute to the general value of the crop. It is now claimed that the yield is easily doubled by the proper varieties and methods of culture.

Investigations of the Irish potato have become very extensive in the effort to secure disease-resistant varieties, especially against potato rot, and to discover the variety best suited to each locality. The relation between races of potatoes and the soil conditions seems to be much more intimate than in the case of most crops. Not only are the well-known varieties under investigation, but also varieties imported from South America and Europe. This work, begun in 1903, has now resulted in the establishment of field stations well distributed through twelve States, from Maine to California. The result of this work upon the total production of this important crop throughout the United States has been very great.

One of the interesting investigations in progress, begun in 1905, is that of the peanut, which is found to be an exceedingly valuable crop in the boll-weevil district of the South. It is claimed that it gives a crop of as great money value as cotton. The alternation of cotton and peanuts is a very effective method of insuring the minimum loss from the boll-weevil.

One of the important pieces of work undertaken by the Bureau is the mapping of fruit districts. This has involved breeding and field work for ten years, and is being extended as rapidly as possible. In a general way, fruit-growers had discovered that certain regions are better than others for certain fruits. The Bureau is mapping these districts definitely, so that a fruit-grower in any region may know the fruits he should attempt to cultivate.

It will be of interest also to know something of the current problems, for these are always suggested by some need that has become apparent. These problems are presented each year in the Year Book of the Department of Agriculture, and some examples from the last two volumes published (1911 and 1912) will indicate the nature and variety of the work that is undertaken.

No problems relating to agriculture are attracting more attention at the present time than soil problems. It is realized that the plant and the soil are partners in production, and that no amount of success in plant-breeding will avail unless there is corresponding success in solving soil problems. The work of the Soil Survey, therefore, in investigating the different soil types of the United States is of fundamental importance. This survey has now described eight soil types, whose distribution covers one-fifth of the arable land of the United States, east of the ninety-eighth meridian, and has discussed the relation of the different soils to crops. It is probably true that each type of soil is especially adapted to the production of some great staple crop or group of crops. Such a survey should result finally in an agriculture so diversified that each area will be made to produce its maximum yield.

The problem of the truck soils of the Atlantic coast region, extending from southern New Jersey well into Georgia, has received special attention. An analysis of these soils has formed the basis of suggestions as to their adaptation to the various truck crops. The detailed advice given as to maximum yields should result in a large increase of total truck-crop production throughout this region.

Bound up with the problem of natural soils is the problem of fertilizers. Concerning this problem there is more diversity of opinion, arising chiefly from the fact that soil chemists too often do not realize the biological and physical aspects of the soil, or the behavior of plants in reference to the soil. One of the most significant undertakings of the Bureau of Soils in this connection is an investigation of the possible sources of potash for fertilizing in connection with what is called intensive agriculture. At the present time the world's supply of potash fertilizer comes mainly from German deposits, and there are reasons why the United States should be independent of this foreign supply if possible. Investigations are in progress to discover a possible home supply, and many suggestions have been made. The Bureau has grouped the possibilities into two categories, which it calls possible minor and major sources. Some of the possible minor sources of the needed potash supply that have been suggested and experimented with more or less are as follows: (1) wood ashes, attention being called to the fact that a vast amount of this material, especially in the form of sawdust and inferior lumber, is supplied by sawmills; (2) wool washings, which are utilized as a source of potash supply in parts of Europe; (3) artificial niter (potassium nitrate), which is manufactured in various parts of the world, notably in India; (4) sunflowers and desert plants, by which waste lands, and especially the arid regions of the country, could be used for growing plants from which potash could be obtained by incinerating the stalks; the plan is suggested by the fact that in Russia sunflowers are grown on waste lands for this purpose; (5) carbonated ponds, many of which, for example, occur in western Nebraska, containing saline waters; (6) rock salts and brines, which occur in a number of deposits and salt wells.

Four possible major sources of potash supply have been suggested. One suggested source is alunite, a potash-containing mineral which is widely distributed in the United States, notable quantities occurring in Colorado, California, Arizona, Nevada, and Utah. The problem involved in this case is to obtain the potash in available form at sufficiently low cost. A second suggested source is from the feldspar and potash silicates, of which there are large deposits, but the methods of extraction have not reached a practical stage. A third suggestion is to obtain the potash supply from the desert basins of the country in which there are heavy deposits of salts. The most promising American source of potash, however, is from the giant kelps of the northwest coast, ranging from California to western Alaska. Investigations as to the occurrence and availability of these kelps have been going on for two or three seasons, and the conclusion has been reached that the supply is ample in amount, having the advantage of being an annual crop, that the crop is easily harvested, and that the most abundant kelps in the region referred to are extremely rich in potash. One of the remarkable facts learned in these investigations is that these kelps pick out and accumulate the potassium salts from the sea water, and not the sodium salts. This really means the use of the ocean as a source of potash supply, the kelps collecting it annually. The general conclusion in reference to these investigations is that there are abundant sources of potash in the United States to supply all the present and prospective needs of agriculture.

During recent years the practice of dry farming has developed extensively, the general principles of which are explained in the chapter treating of soils. On account of the success of this method of handling soil, the expectation has grown rapidly that it will solve the problems of our more arid districts, and that the whole plains region will become a region of successful farms. The Department of Agriculture has felt it necessary to issue a warning, calling attention to some misconceptions concerning dry farming. One of these misconceptions is that dry farming means a definite "system," applicable to any part of the great plains region. Another one is that there can be developed hard and fast rules governing methods of tillage, etc., which can make of dry farming a perfectly definite procedure. Other misconceptions referred to are that deep tillage necessarily increases the water-holding capacity of the soil; that any amount of tillage can be relied upon to overcome the effects of severe and long-continued drought. The danger that is developing seems to be the impression that a farmer may be taught by given rules how to operate a dry land farm anywhere in the plains region. Like any other kind of farming, the problems are local, although there may be general principles that obtain anywhere.

It is interesting to notice that, with the great development of irrigation systems throughout the drier regions, there has now come forward a claim for supplemental irrigation in humid regions. There are frequently great losses of the more valuable crops throughout humid regions from an occasional severe drought, and it is felt to be quite worth while to arrange for supplemental irrigation systems to meet such emergencies.

One of the conspicuous problems of agriculture is the problem of rotation, and perhaps the most important recent experimental work has had to do with rotations in the corn belt. The great corn states are Ohio, Indiana, Illinois, Iowa, Missouri, Kansas, Nebraska, S. Michigan, S. Wisconsin, S. Minnesota, S. E. South Dakota, and W. Kentucky. This area produces two-thirds of the corn crop of the United States, which amounts approximately to two billion bushels a year. The statistics of the past ten years show that the yield of corn, wheat, oats, and hay over this area has been about half what it should be. In consequence of this showing a study of the effect of different rotations was undertaken. For example, the following experiments were carried on: continuous corn culture; corn in rotation with oats; a three-year rotation, consisting of corn, oats, and clover; a four-year rotation, consisting of corn, corn, oats, and clover; and various other modifications of rotations, reaching about ten different kinds. Of course, it was found that continuous crop culture of any one kind is undesirable; also that a rotation of exhausting crops, as oats, barley, and wheat, results badly. The addition of clover or alfalfa in rotation is shown to be a step in advance, and barnyard manure is proved to be the very best fertilizer.

The problem of rotation is also being investigated in connection with insect injuries in the South. The remarkable awakening in agriculture in the South in recent years has resulted in an attempt to diversify the crops. This movement, it is said, is largely the result of the invasion of the boll-weevil. All sorts of crops are attacked by insects, and it is hoped that rotation systems may be developed that will secure what may be called insect control. Various rotations have been experimented with, and the Department is making recommendations as to the most useful kind.

Each year the Department reports promising new fruits. This has been going on since 1901, and therefore a great number of fruits have been presented which are little known among fruit-growers, and which are believed to possess qualities that will make them valuable. The range and number of these new fruits may be indicated by the fact that during 1911 and 1912 the new varieties discussed were as follows: apples, six varieties; pears, two; peaches, one; plums, two; grapes, one; oranges, one; strawberries, one; avocados, one; pecans, five.

Among the notable new introductions into the Southern States are the introductions of new grasses for hay crops adapted to the South, where the natural conditions are not suited to the grasses that are most commonly cultivated for hay. It was found that native species in general are not suitable for such cultivation in the Southern States, and hence several hopeful foreign species were tested. Two of these foreign grasses stood out as of particular importance. One of them is the so-called Rhodes grass (a species of *Chloris*), an African grass named for Cecil Rhodes. This grass has been introduced in Australia, and has become a valuable forage plant, but in this country it seems only adaptable to the extreme South. By far the most important grass for the South is the Soudan grass (a species of *Andropogon*), which is also from Africa, as its name implies. It is wonderfully adaptable to varying conditions, and under all these conditions it produces profitable yields of excellent hay, and can be cultivated with great ease.

One of the aims of the Department during the last few years is to encourage tree-planting by farmers. It appears that farmers are responsible for about 90 per cent. of the one million acres of forest plantations in the United States, plantations chiefly produced in the central treeless region. The Department has issued advice as to the trees for such a region; as to successful methods of planting; and as to proper cultivation.

The whole subject of forestry has also developed the need of seed collection upon a scale never thought of before. It is said that in the national forest reservations there are 15,000,000 acres unproductive, but capable of supporting trees. The present plans contemplate producing forests over this area, which is now bare or covered with brush. It is found that half of these 15,000,000 acres can be reforested only through artificial planting. This means a vast collection of seeds, which, of course, cannot be supplied in any ordinary way. At the rate of 30,000 acres a year, it would take two and a half centuries to plant the 7,500,000 acres. The problem is: Where may these many tons of seed be obtained. The Forest Service has developed a scheme for organizing seed collection upon a stupendous scale. Data in their hands now show that vast quantities of seeds can be secured from the forests for this purpose. The unit that forms the basis of the work is the average of six pounds of seed per acre.

The disease of plants which has attracted the largest attention during the last two or three years is the chestnut bark disease, which was first clearly seen as a source of danger in 1904, when discovered upon Long Island. It has now spread from the general vicinity of New York City, and extends from New Hampshire into Virginia. The disease has been spread rapidly by diseased nursery stock, and up to 1911 the financial loss was estimated at $25,000,000. It appears that this loss is insignificant when compared with that which will ensue if the disease gets into the fine chestnut timber of the southern Appalachians. There seems to be no present indication that the disease is declining in virulence, and it has been found that it kills all trees where it is present long enough. In the absence of any suggestion as to control, the effort now has been to breed resistant races, and this effort has obtained some promising results. Of course, there must be inspection and destruction of diseased nursery stock. The Government is issuing statements that contain advice to growers of orchards and ornamental trees as to such measures of control as seem feasible. It is thought that the outlook is very serious for forest trees.

Perhaps the most significant activity of the Department has been its encouragement of the teaching of agriculture in the high schools. The purpose of this movement does not need any explanation, for it is intended to arouse interest and give some training in our most fundamental occupation, an occupation which should begin to include a far larger number of trained workers. The advance made in agricultural education in the schools is indicated by the fact that sixteen years ago agriculture was not taught in any high school in the United States, and now there are courses given in more than two thousand high schools. The chief advance has been made during the last four years.

SUMMARY

The United States Department of Agriculture has organized eight great divisions of scientific work, the one most immediately concerned with plant-breeding being the Bureau of Plant Industry. The whole range of problems that bear any relation to agriculture are under investigation. Similar work is in progress at sixty-six Agricultural Experiment Stations in the United States. The results of this great volume of investigation are available to everyone in numerous bulletins.

In this chapter illustrations are given of some of the notable achievements of the Bureau of Plant Industry; also some account of the current problems relating to agriculture, problems dealing with valuable crops, forestry, soils, fertilizers, and diseases.

CHAPTER XVIII

THE WORK OF FOREIGN STATIONS

Agricultural experiment stations are numerous in Europe, and they are related to a more intensive agriculture than prevails in this country. Plant-breeding in most of them has followed the older methods of mass culture and hybridizing; in fact, the technic of mass selection has been so highly developed in Germany that it is commonly spoken of as the "German method." Two stations will be selected as illustrations, stations that represent perhaps the most advanced methods and whose results are among the most important. One of them is concerned chiefly with plant-breeding and the other with soil problems.

SWEDISH SEED ASSOCIATION

This is the official designation of the famous agricultural experiment station at Svalöf, Sweden, under the directorship of Dr. Hjalmar Nilsson. This station is notable for its practicable application of the most advanced knowledge in reference to the laws of heredity, and has developed modern methods probably more extensively than any other experiment station. Its work was first brought to the general attention of plant-breeders in the United States by De Vries, in his book entitled "Plant Breeding" (1907), and until recently this book has remained the only source of information, except the station reports, which are all in Swedish, and therefore not generally available. In 1912, however, L. H. Newman, secretary of the Canadian Seed Growers' Association, published an account of the work at Svalöf, based upon a prolonged visit. These two accounts supplement one another, for De Vries lays emphasis upon the scientific principles underlying the methods, and pays scant attention to the details of practice; while Newman presents the practice in great detail, and has little regard for the principles. The chief motive of De Vries was to discover, among the operations of the station, facts which had a bearing upon his theory of mutation as an explanation of the origin of species, and, especially, facts supporting his conception of elementary species. Newman, as a practical plant-breeder, was concerned chiefly with the technic of operations that were yielding such notable results.

One of the noteworthy features of the work of the Swedish station is that it is chiefly concerned with cereals, the great fundamental crops. This is in strong contrast with such plant-breeding as is done by Burbank, for example, which deals for the most part with plants of minor importance. So far as the problem of food supply is concerned, which is our most important material problem, there is no comparison between the importance of cereals and of other crops.

The history of cereals should be appreciated in connection with their breeding. They have been cultivated from the beginning of civilization; in fact, they are often said to have created civilization. Wheat and barley are known to have been cultivated by prehistoric men; oats were added to the cultivated cereals during the period of the lake dwellers; while rye was introduced into Europe during the Middle Ages. Since corn is an American cereal, it does not enter into the work of the Swedish station. The significance of this history is that in the breeding of cereals races are being dealt with that have come down through thousands of years of cultivation. During most of this long period, cultivation has involved unconscious selection, and during the last century this merged gradually into intelligent selection. As a result, the various races are extremely mixed, so that breeding experiments must deal with material that must be disentangled before definite improvements can be made.

During the last half of the nineteenth century, when Darwin's theory of natural selection was dominant, the practice of mass selection was naturally emphasized. As explained in a previous chapter, this method selects all of the best individuals without any attempt to separate the mixture of varieties and strains. The result of such continuous selection is a slow improvement in the average of a mixed population. In this way great improvements have been secured, but very few new things; in fact, it does not provide for selecting out such new things as occur, but merges them with the general average. It is evident that by this method alone an average may be raised to a certain level, but even the best average implies that there are numerous individuals better than the average, so that the highest standard in sight is not attained.

The Swedish station was established in 1886 to produce and improve seeds, at first for southern Sweden and later for all Sweden and Scandinavia. The various races of cereals used in Sweden were deteriorating, so that the work of the station was born of necessity. That this station has developed into our most advanced Experiment Station is due to the character and training of its director. With thorough scientific training he combined great practical insight into the needs of Sweden, so that the program of the station has always been purely practical, designed to meet the immediate needs of the farmers. It will be remembered that the topography of Sweden is extremely diversified, so that a wide range of races or strains is necessary to meet all the conditions. The program of the station, therefore, was to produce races best fitted for every cultural condition in Scandinavia.

At first the long-approved German method of mass selection was used. All hopeful European races were imported and used in the endeavor to secure the desired races by this method. Improvements of old races were secured, but none of the desired new varieties fitted to the peculiar needs of Sweden were obtained. Among the new characters needed for Sweden were stiffer stems, which would stand up better in wind and rain and diminish the heavy loss that came from prostrate and tangled fields of grain. To secure this character, as well as other desirable ones, mass selection was used to the extreme limit of technic, but the results were negative. Of course, some desirable results with various crops were obtained, but in comparison with the needs they were negligible.

Under these circumstances, Nilsson, who became director in 1900, turned his attention to pedigree culture, a method described in a preceding chapter. He discovered that the plant populations he was using in mass selection were a motley mixture, although they were chosen for uniformity. In connection with his selections, he discovered that only the varieties represented by single individuals came true. The conclusion was that pure cultures must be started from single ears, which, of course, means single individuals, rather than from a population of selected individuals. From this suggestion what were called "separate cultures," now commonly called pedigree cultures, were started. Anyone familiar with the bookkeeping necessary in pedigreeing fine animals will realize the enormous amount of bookkeeping that began with pedigree cultures at Svalöf. These records early showed that selected and

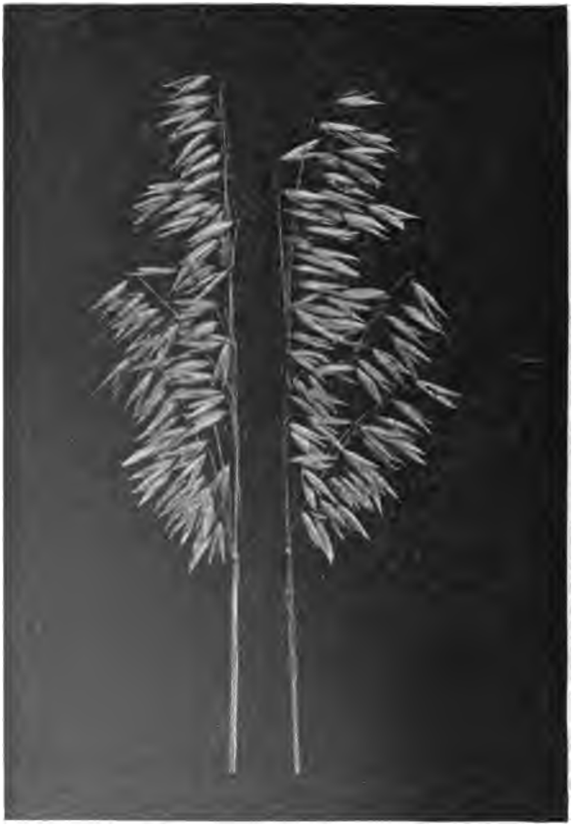

Fig. 105.—Five new varieties of oats produced at Svalöf are illustrated in Figs. 105-109: Fig. 105, flag oats.—After DeVries.

guarded individuals bred true. For example, out of four hundred and twenty-two cultures of oats, made

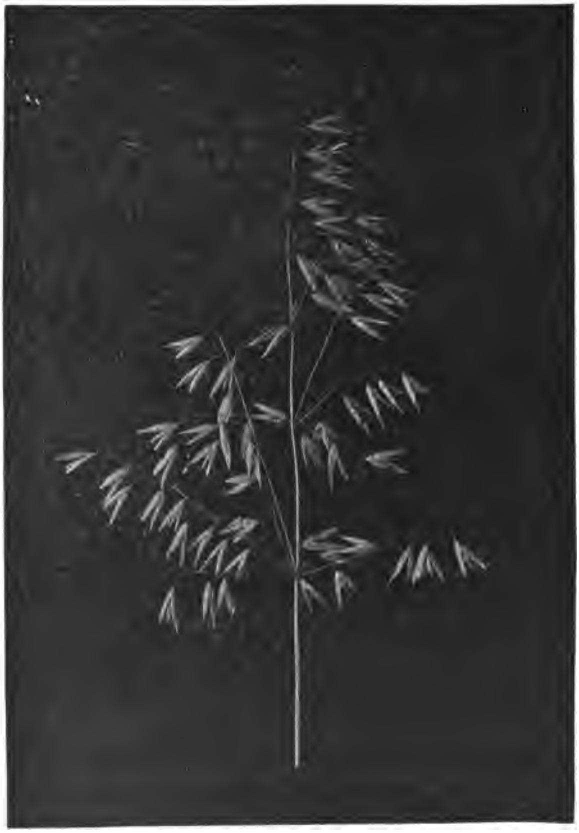

FIG. 106.—Stiff-branched oats.—After DEVRIES.

from selected individuals, three hundred and ninety-seven of them remained uniform. Accordingly, it was

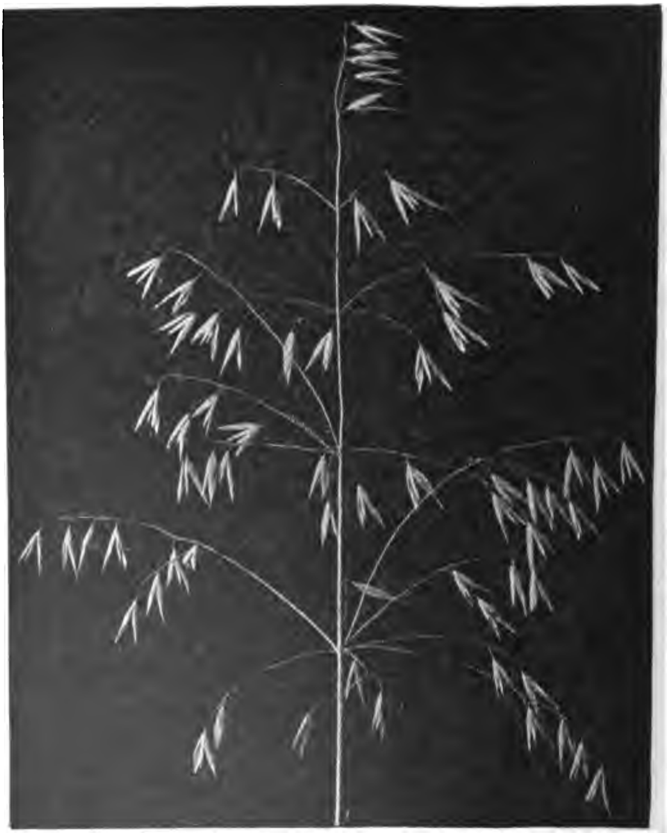

FIG. 107.—Oats with spreading branches.—After DEVRIES.

found that subsequent selection is not necessary to establish the desired variation, but that the initial choice is sufficient.

When the plots of cereals were examined, not as populations but as individuals, the desired races or strains began to be discovered (Figs. 105-109). For example, not only all the desired races of oats became available, but many more besides. This selection of

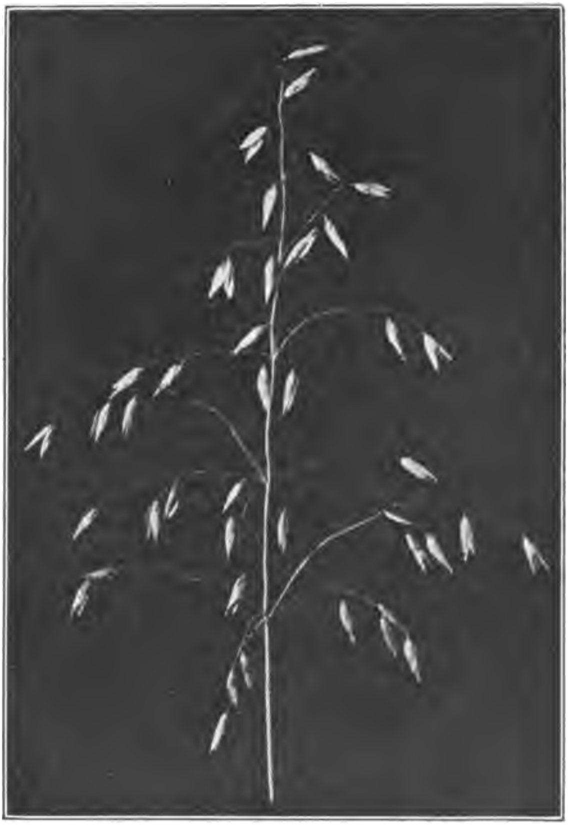

FIG. 108.—Oats with bending branches.—After DEVRIES.

individuals that bred true was the fact that impressed DeVries the most, since it bore directly upon his conception of elementary species. He inferred that there was no need of mass selection and no need of hybrid-

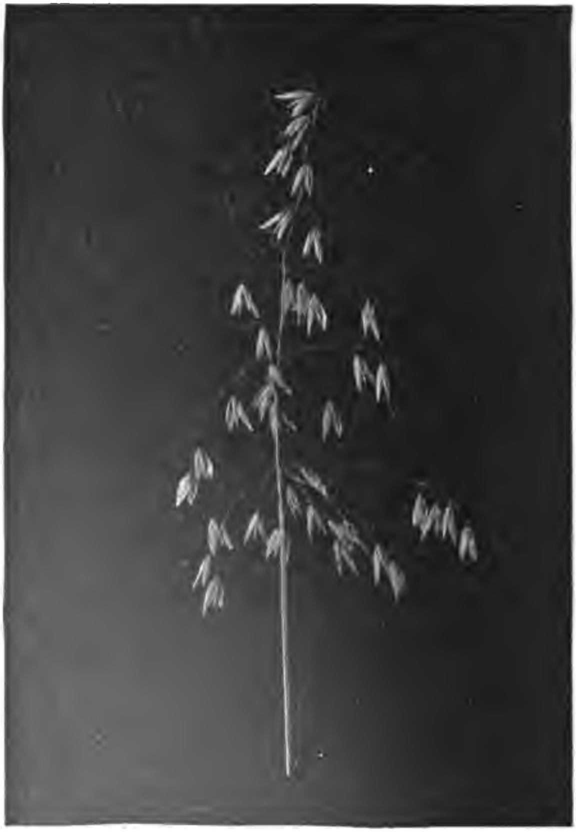

FIG. 109.—Oats with weak branches.—After DEVRIES.

izing; that all that was necessary to do was to select the individual that existed somewhere among the mixed populations.

The operations at Svalöf, however, were by no means restricted to pedigree culture, as successful as its results had proved. It was felt that all methods could be used to advantage, and that each method had its own particular application. In fact, no one method can be regarded as sufficient in plant-breeding, for many more things are needed than the selection of an individual to breed from. The methods in use at Svalöf are in effect four in number.

(1) Pedigree culture is found to be useful in securing rapidly a desired variety, if it exists. So far as experience has gone, however, all the varieties that seem desirable have not been found to exist ready-made. Pedigree culture, therefore, can take advantage only of such desirable forms as do exist.

(2) It was found, further, that desirable individuals cannot always be recognized by morphological characters; that is, one cannot go through a field and select a desirable individual by looking at it. There are physiological differences that are just as important, often more important than morphological ones, so that desirable individuals must be discovered often by testing out.

(3) So far from abandoning hybridization, the Svalöf station uses it as an invaluable method of pro-

ducing combinations that do not exist otherwise. In fact, if the desirable variation does not exist so as to be multiplied by pedigree culture, it is hopeful to attempt to produce it by hybridizing.

(4) Finally, mass culture is very far from being abandoned at Svalöf, but is thought to be very useful in certain cases. Even when a desirable individual can be found and pedigreed, or when a desirable individual is produced as a hybrid, it can usually be improved by mass selection.

It is the combination, therefore, of all of these methods, applied to different situations, that makes for the total success of the operations at Svalöf. The most conspicuous work being carried on may be indicated briefly as follows.

The need was obvious for an autumn wheat in Sweden, which possessed the combination of higher yield, stronger straw, and greater disease-resistance. This need has been partially met by the breeding experiments, a number of excellent pure strains having been isolated from the current mixtures, and then desirable combinations secured by crossing them. As one result, in many districts where rye was the principal crop, because the more important cereal could not be grown, wheat can now be raised with greater profit than rye.

The spring wheat area in Sweden is a very small one, so that spring wheat breeding was undertaken to produce more suitable and profitable varieties for the spring wheat districts. This illustrates the consideration given to relatively small areas that are peculiar in their cultural conditions.

The breeding of oats has represented a very important phase of the work at Svalöf. It was not expected that a single strain suited to all conditions could be secured. The desire has been to increase yield, quality, strength of straw, resistance to disease, and ability to grow vigorously upon a wide variety of soils. A great many pure strains have been isolated and experimented with, but it will take time to secure all the results in view.

Barley is cultivated chiefly in certain provinces, and the station has made great progress in increasing the yield and in meeting the varied conditions.

The breeding of peas, which are chiefly grown as a fodder crop, has also been a feature of the station. Clover and grass breeding began in 1907, and since 36 per cent. of the cultivated area of Sweden is devoted to fodder crops, including grasses and clover chiefly, the problem of these crops has been attacked persistently.

Another conspicuous work is that of potato-breeding, which obviously needed improvement, since the average yield per acre in Sweden was much less than that for the whole of western Europe.

These lines of work will indicate how the station has fitted itself directly into the pressing needs of Sweden rather than undertaken purely scientific problems, or practical problems of minor importance.

ROTHAMSTED

The famous Agricultural Experiment Station which bears this name was established in 1843, and is probably the oldest experiment station with continuous records. The proprietor of the Rothamsted estate in Hertfordshire, England, was Sir John Bennett Lawes, an agricultural chemist, who began some experiments upon the estate in 1837. In 1840 more extensive field experiments were undertaken, and in 1843 he associated with him Dr. J. H. Gilbert. This association began the real history of the station, and these two investigators continued in collaboration for fifty years. At this station, therefore, there are continuous records for almost three-fourths of a century, and the records have largely to do with soil investigations. In 1856 the experiments were enlarged to occupy forty acres, and over that area, ever since, the experiments have been going on and the records have been kept. In 1889 Sir John Lawes transferred his laboratories and fields to a Board of Trustees, with an endowment, insuring continuance of the investigations.

It is at Rothamsted, therefore, that there is found the greatest mass of continuous records in reference to soil fertility, in existence. These records are of inestimable value in reaching conclusions in reference to various soil operations. The mass of records is so large that the temptation has always been for a student to discover in them data to substantiate his own views. Like any other large mass of records, they can be used to confirm a great variety of conclusions. The value of these records, therefore, consists in their continuity through so long a period of time, and their availability as a basis of conclusions, rather than in any of the conclusions that have been drawn.

As an illustration of the character and extent of the records, the following statements may be made. There are rotation records since 1848, showing the effect of long-continued crop rotation, not available anywhere else. There are also records of wheat grown on the same field continuously since 1844; and this can be contrasted with records of wheat alternating with fallow conditions since 1851. There is a record of continuous barley culture since 1851; a record of potato culture for twenty-six years; a record of continuous hay culture since 1856; and of root crops since 1845.

Certain general conclusions may be drawn from these records, which have become a part of current belief and practice, especially those that have to do with the rotation of crops. Furthermore, it is established that rotation alone does not maintain fertility, and that if dependence were placed upon rotation the yield of most of the crops gradually declined. In contrast with crop rotation is the alternation of crops and fallow fields, and the records indicate that this cannot be depended upon exclusively, since the yield gradually declined. The data concerning fertilizers can be interpreted variously, and therefore has led to divergent conclusions. The chief trouble in reference to such conclusions is the effect of various fertilizers which have not been analyzed so as to determine whether their effects were direct or indirect, or whether they had to do with certain soil conditions which do not obtain at all times.

SUMMARY

The two foreign experiment stations selected as representative are the Swedish station at Svalöf, where plant-breeding is conducted according to the most advanced scientific methods, and the English station at Rothamsted, where chief emphasis has been laid upon soil problems.

The Swedish station is concerned primarily with the crops of immediate importance to Sweden, and at this station the first extensive use of pedigree culture was made. This does not mean that the older methods of mass selection and hybridizing have been abandoned, for all methods are used as they are found to be useful. The advantage of pedigree culture is defined at this station as useful in securing rapidly a desired variety if it exists; but hybridizing is also used as an invaluable method of producing a useful variety which does not exist otherwise.

The Rothamsted station is the oldest agricultural experiment station with continuous records, having been established in 1843. At this station there is found the greatest mass of records relating to soil fertility, in existence. From these records general conclusions have been drawn which have become a part of current belief and practice, especially in reference to the rotation of crops.

CHAPTER XIX

THE SOIL

Every practical plant-breeder to-day must know much more about the soil than was once thought to be necessary. To most people the soil is simply a kind of dirt from which plants can get food. The recent development of our knowledge of the soil has shown it to be a very complex thing in its relationship to plants. Whenever advantage is taken of such knowledge as we have, the results on plant growth have been remarkable. In our ordinary garden and farm operations we have been in the habit of breaking up the soil, committing seeds to it, and then trusting to nature to do the rest. We have depended rather blindly upon the soil as a natural resource, much as a mine, which needs no special cultivation.

The new knowledge, in reference to the soil, has been applied in Europe more generally than in the United States, and the results are already apparent. When it is known that the average wheat yield in the United States is thirteen bushels an acre, and that the average yield in Europe has become thirty-three bushels an acre, it becomes apparent that the application of our knowledge of the soil is worth while. The Americans have accustomed themselves too long to the idea of their boundless resources. They must now begin to use some intelligence, so that our resources will show a much larger yield. Even though the United States is about the youngest large country in cultivation, we hear already of ''worn-out'' farms, especially in New England. To say that farms can be worn out in fifty or one hundred years is merely to say that they have not been farmed intelligently. When it is known that successful agriculture has been conducted continuously in Palestine for thousands of years, in a relatively sterile country, and that the farms are not worn out there yet, it shows that something is wrong with American farming. The best approach to some knowledge of the relation of soil to plants is to consider first what plants need, and then what the soil supplies.

WHAT PLANTS NEED

It is not necessary to attempt to give the needs of plants in order of importance. All of the real needs of a plant are important.

Oxygen.—Of course, plants need the oxygen of the air for the same reason that animals need it, and it is evident that it is supplied in abundance for the parts above ground, wherever plants are cultivated. The important thing to remember, therefore, is that there are living and working parts of the plant imbedded in the soil, and most plants are started by seeds buried in the soil, and here the problem of free oxygen supply calls for our help. If the soil spaces are filled with water the air is excluded; if the soil is packed too firmly the air cannot circulate; or if there is too much clay the air is not free to move. All such conditions must be remedied if plants are to do well. The water must be drained off; the soil must be loosened up, and the impervious clay must be mixed with something that will give a looser texture to the soil. One of the most common blunders in planting seeds where artificial water is employed is to use too much water, so that plants are in a " puddle " and the air is excluded.

Light.—It is well known that the plants we cultivate need light, but this does not mean that bright sunlight is necessary. Very ordinary light seems to be sufficient. It is evident, therefore, that cultivated plants are not likely to lack light. The danger that comes to plants, however, is not from lack of sufficient light so much as lack of the presence of certain active rays of light used by plants in the manufacture of food. When light passes through smoke, its usefulness to plants is very much diminished, and this becomes a serious problem in the neighborhood of factories and in smoky towns and cities. When light has passed through leaves, the necessary active rays have disappeared entirely, so that plants cannot grow completely shaded by other plants.

It is a wise thing, therefore, to see to it that plants under cultivation are not densely shaded by other plants.

Heat.—The favorable condition of temperature varies for different plants, and for the different periods of the same plant. In general, a lower temperature is more favorable for a seedling than for a maturing plant, and this fact is recognized in the spring sowing and summer harvesting of ordinary crops. The variation in the temperature requirement of different seedlings also explains why some seeds are planted earlier than others. The successful extension of crops into different latitudes has depended upon securing varieties with different temperature ranges. For example, during the last ten years the agricultural experiment stations of Canada, by coöperative effort, have succeeded in extending the wheat belt northward approximately a degree of latitude each year, which in that country means a tremendous extension of area each year. The results of passing beyond the best temperature range in either direction are soon obvious in a plant. If the temperature is low, the plant grows very slowly; if it is too high, the plant usually becomes tall and slender; and in both cases its lack of vigor is shown by the fact that it is unusually subject to disease.

Water.—Water is not only the necessary condition for plant work, but also a necessary material used in the manufacture of plant food. The active plant body is really saturated with water, and the living substance (protoplasm) cannot work effectively unless it contains an abundance of water. In addition to the water that puts a plant in working condition, a much smaller amount is used in the manufacture of carbohydrates (sugars and starches) by the leaves. A saturated plant exposed to the air means a continual loss of water from its free surface, and notably from its leaves. This loss of water must be made good by the continual entrance of the water of the soil into the roots, so that there is a continual movement of water through the plant. When the loss of water exceeds the supply, the immediate effect on the plant is seen in its wilting. In the case of large field crops there is no control of the water supply, and the farmer takes his chances that the rainfall will be adequate; but in gardens it is usually possible to supplement a failing water supply, and also in regions of irrigation the water supply is under control. In all cases where water is supplied in some way, it is necessary to learn the needs of the crop. Generally too much water is supplied, which injures both the plant and the soil. It should be known also that the amount of water required varies with the period of the plant. For example, more water is needed during the growth of the plant than during either seed germination or ripening. The problem, therefore, is not merely to induce plants to grow by just keeping them from wilting, but to enable them to grow vigorously. Too little water during the growing period results in smaller leaves and less work; while a supply of water that favors vigorous growth, if continued too long, will delay ripening.

Carbon dioxide.—Carbon dioxide must be ranked with water as of first importance, because these two materials are the ones used in the manufacture of carbohydrates. Since carbon dioxide enters the plant from the air, its supply is usually sufficient, and in any event there is nothing to do in the way of regulating the supply.

Soil salts.—Probably chief among the materials obtained from the soil (excluding water) are the compounds of nitrogen. Although nitrogen forms a very large part of the air, it cannot be used by plants in its free condition, but must be obtained from certain of its compounds, chief among which are the nitrates. It is evident, therefore, that nitrates must exist in the soil if plants are to grow, and that if they become insufficient for any reason they must be restored. The nitrates may not only be insufficient in amount, but they may be excessive in amount, so that too much, as well as too little, is injurious to the crop. This fact applies to most things that plants need, which cultivators do not appreciate fully.

Numerous other salts are needed by plants in one way or another, as compounds of phosphorus, sulphur, potassium, calcium, magnesium, iron, etc. What these substances enable the plant to do is known in some cases, but in others the particular use has not been discovered.

Toxic substances.—Of course these are not what plants need, but they may be considered in this connection. It is not only necessary to determine whether the soil contains the substances plants need, but also whether it contains substances injurious to the plants we wish to cultivate. For example, a soil may contain too much acid or too much alkali, and must be treated accordingly. Compounds of metals getting into the water supply in the waste products drained away from industrial establishments may be very injurious to plants. Gases of various kinds diffused through the air from manufacturing establishments are often very destructive to plants, or prevent vigorous growth.

Limiting factors.—In cultivating plants we are not dealing with one condition or one substance, but with a complex of conditions and substances. These may be spoken of as factors that have to do with successful plant growth. It is a very common mistake to suppose that, if some one factor is supplied, plants will do well. For example, some will say that a proper water supply will insure good plants; others will claim that a supply of nitrates is all that is necessary for plants to do well; while others insist that if phosphates are supplied all will be well. From this point of view a great number of so-called "fertilizers" have been devised, each claiming to supply all plants with whatever they need. It must be evident that any factor, or even several factors, may be favorable, and yet the plant cannot do well if any one necessary factor is unfavorable. In other words, a plant cannot do any better than the most unfavorable factor permits, and such a factor is called a *limiting factor.* For example, the necessary nitrates may be supplied, but if the water supply is too scanty or too abundant, the water is a limiting factor, and the nitrates cease to be serviceable. In another case the water supply may be just right, but if the nitrates are not just right they are a limiting factor and impede the plant, in spite of a good water supply. In this way each factor in turn may become a limiting factor.

Any one of the half dozen or more factors, therefore, may be a limiting factor, and it is the limiting factor that determines the success of a plant. It is like a group of men walking. The group as a whole advances no more rapidly than the slowest walker. In other words, the slowest walker is the limiting factor. When plants are not doing well, therefore, the course to pursue is not to apply some treatment that is claimed to be a "cure-all," but to discover, if possible, the factor that is holding back the usefulness of the numerous factors that are all right. A plant that is not doing its best is like a train moving with brakes set, and the thing to discover is the factor that is acting as a brake.

WHAT THE SOIL SUPPLIES

The structure of the soil must be considered from three aspects: chemical, physical, and biological.

Chemistry of the soil.—The soil is a mixture of various substances that have come from various sources. The ordinary material and the relatively permanent material has come from rocks in various ways. When it began to be covered with vegetation, the plants contributed their bodies to the mixture, and so there was a slow accumulation of humus, which gave a dark color to the soil mixture. The differences among soils are brought about by the various proportions in which these substances occur in the soil mixture. Soils are spoken of as sandy soils, clay soils, lime soils, humus soils, etc., because they are rich in sand, clay, lime, humus, etc. It should also be remembered that these numerous substances react upon one another in ways that are intricate and poorly understood, so that the soil in this respect may be thought of as a chemical laboratory where work is going on continuously.

Physics of the soil.—The physical properties of the soil are extremely important, and it is a subject of great difficulty on account of the complex mixture. One of the most important physical properties of the soil is its relation to water. In fact, the capacities of soils to receive water and to retain it in an available condition for plants is the most obvious physical feature that cultivation of the soil seeks to control. A simple illustration of the problems involved may be used in the case of the clay constituent of the soil. A certain amount of clay interferes with the free movement of water, and therefore prevents it from draining away too rapidly. It thus increases the retentive power of the soil, but an excessive amount of clay interferes too much with the movement of water and results in a water-soaked soil, which excludes the air.

The humus of the soil greatly increases its water-holding capacity. In fact, a forest soil, in general the best example of a humus soil, has the physical properties of a sponge in receiving and retaining water.

Biology of the soil.—The soil has been called a biological laboratory because it contains multitudes of exceedingly minute plants (chiefly bacteria) and animals. The bacteria of the soil have come to be recognized as most important agents for putting the soil in proper condition for such plants as we cultivate. Bacteria are active in all decompositions of organic material, which is thus reduced to substances which plants can use. Conspicuous among their activities, however, is their relation to the nitrogen supply of the soil. Certain bacteria can use free nitrogen of the air, and in this way the nitrogen enters into compounds that cultivated plants can use. It is evident that, since plants must always have a nitrogen supply from the soil, this work of the nitrogen-fixing bacteria is of the first importance.

In removing crops, the nitrogen compounds obtained by the plants from the soil are removed also, and if there were no way of restoring these compounds the soil would sooner or later become so impoverished that it could not produce a good crop. In other words, it would result in a nitrogen famine. If a field has become reduced to the point of a nitrogen famine it may be restored to usefulness by resting for a time until the bacteria have restored the nitrogen compounds. The resting of a field, that is, not working it for a crop, is called letting the field "lie fallow."

The restoration of nitrogen compounds in this way, however, is usually too slow a process for our purpose. A much more rapid way is by means of the "rotation of crops." It is found that soil is kept in much better condition as to nitrogen if the same crop is not grown continuously upon it. Crops vary as to their wastefulness of nitrogen, so that if a crop that removes a minimum amount of nitrogen compounds alternates with a crop that removes the maximum of these compounds, a nitrogen balance may be maintained by the bacteria. By far the most effective rotation is secured by using leguminous plants as the alternating crop, notably the clovers and alfalfa, for these plants add nitrogen compounds to the soil, through their peculiar association with nitrogen-fixing bacteria.

Conclusions.—There are some conclusions that follow from a consideration of these three aspects of the soil that should be mentioned at this point. The preceding paragraphs have given only a glimpse of the complexity of the soil, with its chemical constituents, its physical properties, and its active bacterial life. It is a great complex, in which changes are always taking place, and which can be thrown out of balance in a number of ways. Left to itself and to natural vegetation, the soil becomes better for plants with each succeeding year, but, interfered with by man, it frequently gets into bad condition. This is notably true when attempts are made to remedy unknown troubles by using unknown fertilizers, especially unknown chemicals, which are as dangerous to the soil in the hands of inexperienced people as are strong medicines in the hands of the untrained. It is obvious that any efficient manipulation of the soil, especially in adding materials to it, requires experience and considerable knowledge.

Tillage.—All of the processes included in "breaking up" the soil come under the head of *tillage,* the purpose of which is to put the soil into the best possible physical condition. The breaking-up of the soil for planting seeds is known to everyone, but its purpose is not widely understood. Many suppose it is only a way of getting seeds into the ground, but that is the least important of its purposes. Its real purpose is to pulverize the soil because finely pulverized soil is in the best physical condition for plants to secure a good circulation of air, which is essential to the best plant growth, and to enable the soil to hold a much larger amount of moisture. The smaller the soil particles, and the closer together they are, the more water will the soil hold. The capacity of the soil for water, therefore, is in proportion to the minuteness of its particles. This combination of small particles and free circulation of air is an ideal combination for productive soil. Of course, pulverizing the soil also improves its drainage, and so permits free circulation of air.

After the soil is well pulverized and the seeds are sown, the work of tillage is not at an end. The physical conditions that favor germinating seeds also favor growing plants; therefore, the soil must be kept in good physical condition. An additional advantage of tillage to growing plants is the conservation of moisture. Water not only drains away from the soil, but it also evaporates from the surface. If the surface becomes caked it must be broken up and pulverized, so that the soil can get a new grip on the water, or the loss will be serious. Tillage, therefore, checks evaporation as well as loss by drainage. In fact, in dry farming it has been found that a shallow pulverized layer of soil acts like a "mulch" in checking evaporation.

It must not be thought that the only water available for plants is that which is held by the soil particles with which their roots come into contact. A most important fact is the capillarity of the soil. This means that when films of water held by the soil particles become thinner because some of the water has entered the roots, there is a rearrangement of the water in all the neighboring films. Water is pulled away from a thicker film to a thinner one, and this starts a movement of water from every direction toward the thinner films. Therefore, as water is lost from the soil by evaporation or by passing into root systems, there is a movement of water toward the surface from the deeper parts of the soil. This is the so-called capillary movement of water. The available water for plants, therefore, is all the water in the neighborhood that is free to move through the soil.

It is a very common mistake to suppose that the only soil salts available are those with which the roots come in contact. What has been said concerning the capillary movement of water through the soil should correct this impression. The moving water contains the salts in solution, and therefore the salts are also moving toward the surface continually and being deposited in the surface soil. It must be remembered that this movement is not only toward the points where the water and salts are entering the plants, but also toward the general surface from which the water is being evaporated. This means that the salts available for plants are not only those which happen to be within the surface soil at a given time, but also all that are within reach of the water movement.

There is a general impression that if a sample of soil be sent to a chemist to analyze, he can discover what it lacks and prescribe a suitable fertilizer. If the statements of the preceding paragraphs are true, it is evident that no such chemical analysis can tell what the soil of any farm needs. In the first place, the appropriate materials are found in all soils upon which natural vegetation can grow. Soil is a variable mixture and there is no fixed standard that determines the best mixture. In the second place, the immediate need of any soil is to be put in proper physical condition, and what is necessary to accomplish this can be told only by an examination of the area; it certainly cannot be told from a sample.

SUMMARY

There is great need to take advantage of all the increasing knowledge in reference to the soil. Where this knowledge has been applied the yield has been increased remarkably. To treat the soil as a natural resource, to be drawn upon but not conserved, is a reckless waste.

From the soil, plants obtain water, which is necessary to keep them in working condition, and is also a material used in the manufacture of carbohydrates. Certain salts of the soil are also necessary, chief among which are nitrates, phosphates, sulphates, potash, and lime.

In the soil there may also exist toxic substances; that is, substances injurious to cultivated plants. For example, a soil may be too acid or too alkaline, so that it must be neutralized.

No single factor can determine that a plant will do well. No matter how many factors are right, a plant can do better than its most unfavorable factor permits. Such a factor is called a *limiting factor.* When plants are not doing well, therefore, there is no "cure-all" which will remedy the situation; but the limiting factor must be discovered and treated. This means that a diagnosis of the soil trouble is of the same scientific order as the diagnosis of a human disease, and that prescriptions must vary according to the limiting factor.

The soil is a very complex mixture, with its chemical constituents; its physical properties, especially those relating to its capacity for receiving and retaining water; and its microscopic flora and fauna, very essential for keeping the soil in condition. Anything that disturbs this chemical, physical, and biological balance may modify the soil very unfavorably for plants.

Tillage consists in putting and keeping the soil in the best physical condition. The best physical condition is a finely pulverized soil, for pulverization increases the water-holding capacity, checks the loss of water by evaporation from the surface, and secures good drainage and free circulation of the air.

As water of the soil passes into plants, and evaporates from the free surface of the soil, there is a capillary movement of water through the soil toward the regions of loss. It follows that the water available for plants is not only that in immediate contact with their roots, but also the whole supply of water that is free to move through the soil.

The capillary movement of water toward the surface of the soil is also the occasion of the movement of soil salts in solution. These salts are continually moving toward the surface of the soil, where they are deposited as the water evaporates. The salts available for plants, therefore, are not merely those in the soil which the roots occupy, but all those within reach of the capillary movement of water.

No chemical analysis of the soil can determine its needs, which are usually related to its physical condition. The needs of a soil can no more be diagnosed apart from its habitat than the needs of a sick person can be diagnosed in the absence of the patient.

It will be necessary to train a race of professional soil experts, whose function will be fully as scientific, and far more important, than the function of physicians.

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